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Middle-Ear Ossicles of the Multituberculate *Kryptobaatar* from the Mongolian Late Cretaceous: Implications for Mammalian Relationships and the Evolution of the Auditory Apparatus*

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ABSTRACT

Partial malleus, ectotympanic, and stylohyal along with a fragment of a possible stapes are described for the multituberculate *Kryptobaatar dashzevegi* from the Late Cretaceous of Mongolia. The malleus, represented by the anterior process (composed of the goniale), is attached and only partially delimited by sutures from a segment of the anterior crus of the ectotympanic. The possible stapes fragment may be part of a crus of a stirrup-shaped bone.

After comparison of these elements with those of other mammalian forms, a matrix of 62 characters of the ossicles and basicranium across 19 taxa was compiled and analyzed with PAUP. Four equally most parsimonious trees were obtained, which differ in the relationships of multituberculates, monotremes, and triconodonts with regard to the prototribosphenidan lineage. Monotremata is either the sister group of Theriiformes (Multituberculata + Theria) or united with Multituber-

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culata in a monophyletic grouping. Because the ossicles are poorly or wholly unknown for most of the taxa considered, their phylogenetic bearing is limited.

The phylogenetic information derived from the transformations of the postdentary bones/ear ossicles and the dentition is not congruent. Our cla-

distic analysis suggests that definitive middle-ear ossicles evolved in the last common ancestor of multituberculates, monotremes, triconodonts, and trechnotherians (symmetrodonts + therians) and that the triangular molar cusp pattern of kuehneotheriids and trechnotherians is likely convergent.

INTRODUCTION

The Reichert-Gaupp Theory (Reichert, 1837; Gaupp, 1913) summarizes our understanding of the homologies of the postdentary bones of non-mammalian amniotes with the middle-ear bones of mammals (for modern reviews see Moore, 1981; Starck, 1979; and Novacek, 1993). The transformation of lower jaw elements into auditory structures, one of the hallmarks of Mammalia (*sensu* Rowe, 1988, the clade including the common ancestor of extant mammals and all its descendants), had far-reaching repercussions for the origin and subsequent evolution of the mammalian skull. Regions of the head thought to have been notably modified include the basicranium, the lateral wall of the braincase, and the masticatory apparatus (Allin, 1975; Crompton and Hylander, 1986; Maier, 1987, 1993; Kuhn and Zeller, 1987; Allin and Hopson, 1992).

The formation of an ossicular chain transmitting sound from the outer to the inner ear from former load-bearing elements of the lower jaw can be traced in the fossil record as well as in the ontogeny of living mammals (Reichert, 1837; Gaupp, 1913; Allin, 1975; Maier, 1990). The bony elements involved in mammals (and their homologs in non-mammalian amniotes) are the ectotympanic (angular), malleus (articular and prearticular or goniale), incus (quadrate), and finally, the stapes (columella auris or stapes). To date, our understanding of the fate of the postdentary bones represents one of the most successful interplays between paleontology and embryology in establishing the major features of a complex evolutionary event. Nevertheless, aspects of this transformation are still questioned, and radically new hypotheses (Jarvik, 1980) departing from the classic Reichert-Gaupp Theory and its modern formulation (Allin, 1975, 1986; Allin and Hopson, 1992) have been proposed.

The complex history of the mammalian

middle-ear ossicles is suggested in the heterogeneous origin of the involved elements, which include dermal ossifications (the ectotympanic and the anterior process of the malleus) and derivatives from the mandibular or first arch cartilage (the articular portion of the malleus and the incus), the hyoid or second arch cartilage (most of the stapes), and the auditory capsule (part of the stapedia footplate) (Gegenbaur, 1898; Gaupp, 1908, 1913; Anson et al., 1960). This complex provides a wealth of anatomical variation that is widely accepted to be of significance for systematic and functional analyses (Fleischer, 1973, 1978; Novacek and Wyss, 1986; Gaudin et al., 1996). Yet, study of the early evolution of this system in the fossil record has been hampered by the exceedingly fragile nature of the middle-ear bones, which are only loosely attached to the skull base. A bony bulla, which as a rule encloses the middle ear and protects the ossicles in living therian mammals, is lacking in most early mammals. Consequently, middle-ear bones are almost never preserved in Mesozoic mammals, even in fully articulated specimens. The only ear ossicles reported from Mesozoic mammals are the stapes, malleus, and incus of the multituberculate *Chulsanbaatar* (Hurum et al., 1995) and the stapes of an indeterminate placental (Archibald, 1979); both are Late Cretaceous in age.

Basal Mammaliaformes (*sensu* Rowe, 1988, the clade including the common ancestor of *Morganucodon* and Mammalia plus all its descendants) ought to play a prominent role in the elucidation of competing hypotheses about the origin of the mammalian auditory apparatus, because theoretically they can provide characters and combination of characters not present among living taxa (Gauthier et al., 1988; Donoghue et al., 1989). Fossils also can provide the historical

succession of events, permitting determination of minimal ages for character transformations (Novacek, 1992c; Norell, 1992; Norell and Novacek, 1992; Smith, 1994). Unfortunately, the available information on middle-ear bones in Mesozoic mammals is so deficient that these elements have played an almost negligible role in our understanding of early mammal relationships. A few characters, such as postdentary bones attached to lower jaw, or suspended from cranium, have been used for phylogenetic purposes (Rowe, 1988; Wible, 1991). However, characters so general do not adequately reflect the numerous character transformations that ought to be expressed in a phylogenetic analysis. Better preserved material and detailed descriptions are needed so that these elements can be included in the reconstruction of the overall framework of mammalian evolution.

We provide here the first substantial evidence of the malleus and ectotympanic in Mesozoic multituberculates, derived from *Kryptobaatar dashzevegi* from the Late Cretaceous of Mongolia. Our description of these elements furnishes us the opportunity to compare them with the ear ossicles previously described in other multituberculates, i.e., the Late Cretaceous *Chulsanbaatar* (Hurn et al., 1995) and the apomorphic Paleocene taeniolabidid *Lambdopsalis* (Miao and Lillegraven, 1986; Miao, 1988; Meng, 1992; Meng and Wyss, 1995), and in living mammals. In addition to the fragmentary malleus and ectotympanic, we also describe a probable fragment of stapes and the stylohyal in *Kryptobaatar*. Finally, a discussion of characters from the auditory region of multituberculates and other early mammals is presented.

MATERIALS AND METHODS

Multituberculates are the most abundant mammals found in the Late Cretaceous of Mongolia. To date, more than 240 specimens have been collected by the Joint Paleontological Expedition of the Mongolian Academy of Sciences and the American Museum of Natural History. Dashzeveg et al. (1995) reported 169 multituberculate specimens from a single locality alone, Ukhaa Tolgod,

and the number has increased since that report was submitted. As of that report, multituberculates represented over 80% of all mammal skulls and skeletons collected from this extremely rich locality.

All Asian Late Cretaceous multituberculates have been assigned to Taeniolabidoidea. *Gobibaatar parvus*, originally described as a ptilodontoid (Kielan-Jaworowska, 1970), is now regarded as a junior synonym of *Kryptobaatar* (Kielan-Jaworowska, 1980). At present, eight monospecific genera of multituberculates are recognized from the Mongolian Late Cretaceous. However, *Tugribaatar saichaenensis*, known only from the type specimen, an incomplete skull and lower jaws (Kielan-Jaworowska and Dashzeveg, 1978), is likely a junior synonym of *Kryptobaatar* (Rougier, Novacek, and Dashzeveg, in prep.).

Most of the multituberculates collected from the Gobi Desert by the Mongolian-American Expedition, including the two specimens described here, are referable to *Kryptobaatar dashzevegi* (Kielan-Jaworowska, 1970), the most abundant mammalian taxon from the Djadokhta Formation (Kielan-Jaworowska, 1974). The first of these specimens, cataloged as PSS-MAE-113 (fig. 1) in the Geological Institute, Ulaan Baatar, was found in Tugrugen Shireh, also called Toogreeg. This well-known locality (Kielan-Jaworowska and Dashzeveg, 1978) has yielded numerous mammal and dinosaur remains, including the famous fighting dinosaurs (Kielan-Jaworowska and Barsbold, 1972; Osmolska, 1993). Toogreeg strata are considered to be contemporaneous with those from the type locality of the Djadokhta Formation at Bayn Dzak (Shabarakh Usu), and the Djadokhta is thought to be of possible Campanian Age (Jerzykiewicz et al., 1993; Dashzeveg et al., 1995). The second specimen, PSS-MAE-101 (fig. 2), illustrated by Dashzeveg et al. (1995: fig. 3), comes from the newly discovered locality of Ukhaa Tolgod. This locality shows a lithologic sequence and faunal content strikingly similar to that of the type section of the Djadokhta Formation. The age of Ukhaa Tolgod relative to the Djadokhta and the allegedly younger faunas of the Barun Goyot Formation (Grad-

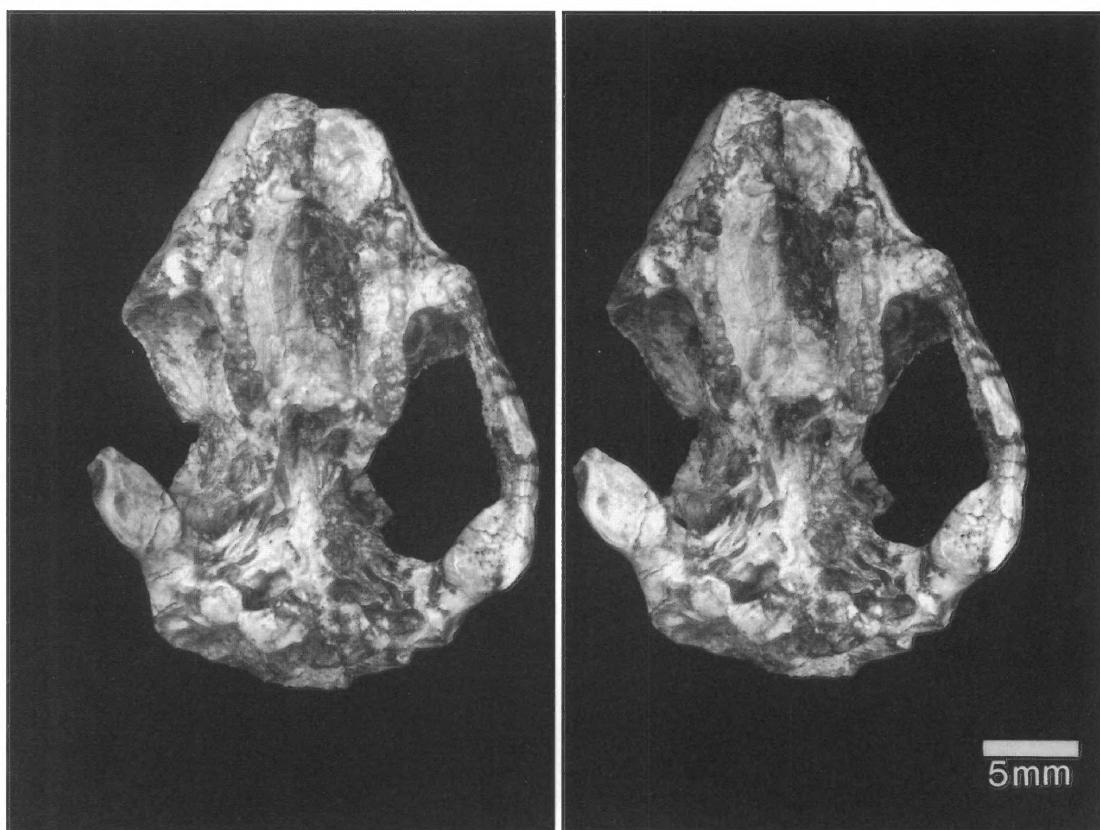


Fig. 1. Stereophotograph of the skull of *Kryptobaatar dashzevegi* PSS-MAE-113 in ventral view.

zinski et al., 1977) is, however, not yet known.

PSS-MAE-113 is a well-preserved skull associated with the right lower jaw. Parts of the left zygomatic arch, the left lateral wall of the braincase, and part of the cranial vault are missing. PSS-MAE-101, a slightly smaller individual, consists of the anterior half of a fully articulated skeleton and includes a pristine skull and lower jaws, as well as remains of the anterior portion of the vertebral column, both shoulder girdles, and forelimbs. Although this specimen has not yet been fully prepared, the morphology exposed agrees with that of *Kryptobaatar*.

Our use of anatomical terminology follows Fleischer (1973, 1978) and Kielan-Jaworowska et al. (1986), with additions and changes suggested by Wible (1990), Rougier et al. (1992, in press), Wible and Hopson (1993, 1995), and Wible et al. (1995). The

taxonomic units employed here follow definitions by McKenna (1975), Prothero (1981), Rowe (1988, 1993), Simmons (1993), Rougier (1993), Hopson (1994), and Rougier et al. (in press).

Abbreviations

AMNH	American Museum of Natural History, Department of Mammalogy
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing
MAE	Collections of the joint Mongolian Academy of Sciences-American Museum of Natural History Paleontological Expeditions
PSS	Paleontological and Stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar
YPM-PU	Yale Peabody Museum, Princeton University Collection, New Haven

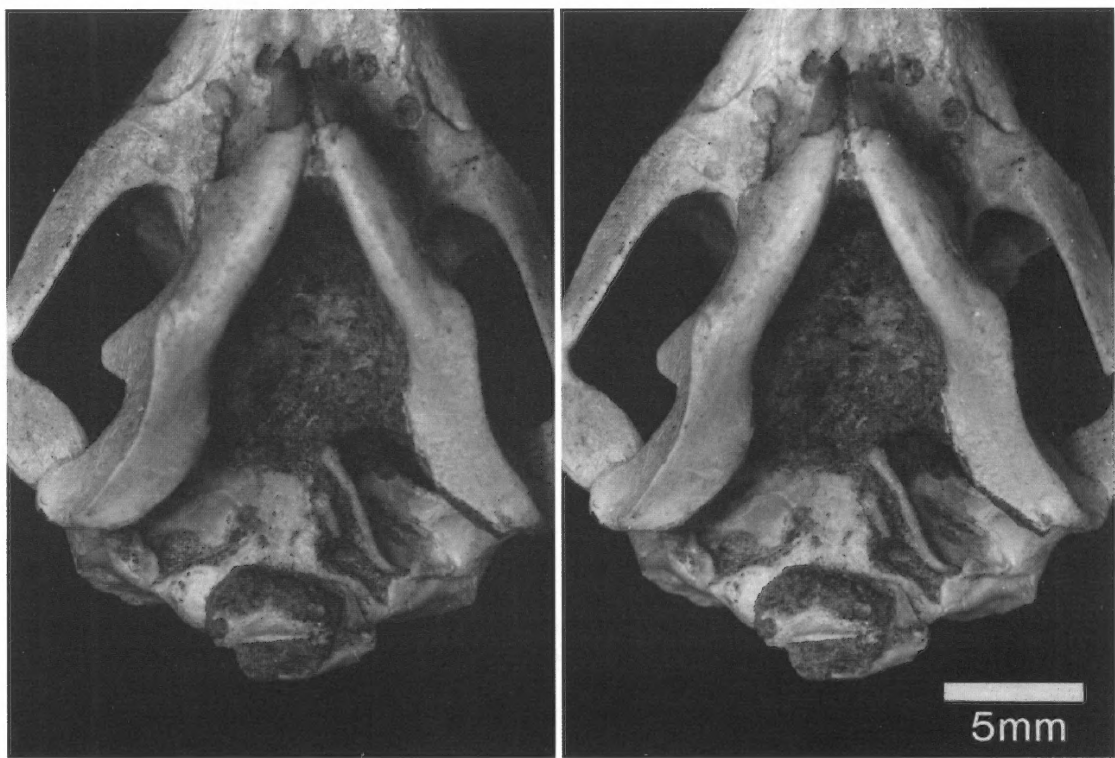


Fig. 2. Stereophotograph of the skull of *Kryptobaatar dashzevegi* PSS-MAE-101 in ventral view.

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DESCRIPTIONS

Both specimens of *Kryptobaatar dashzevegi* (PSS-MAE-113 and 101) reveal aspects of the ear region; the first shows remarkable preservation of the ear ossicles: fragmentary malleus and ectotympanic on the right side of the skull and a probable fragment of the stapes on the left.

MALLEUS AND ECTOTYMPANIC (FIG. 3)

As preserved, the partial malleus and ectotympanic of PSS-MAE-113 form a massive, rodlike structure broken at both ends, with the malleus situated posteriorly and the ectotympanic anteriorly; the contact between the two is not demarcated fully by sutures. These elements were preserved in the right epitympanic recess, but they appear to have been overturned, that is, rotated 90° or more about the long axis. Therefore, the surface

exposed in ventral view is actually the dorsal or medial side. Supporting our interpretation is the ventral exposure of a distinct foramen for the passage of the chorda tympani nerve in the malleus, which in living mammals lies either on the dorsal or medial surface of the anterior process of the malleus (Henson, 1961; Zeller, 1993). In spite of this rotation, the long axis seems to have retained the approximate life position. The malleus and ectotympanic of PSS-MAE-113 are described here in position as they are preserved. Additionally, we provide a likely restoration of the missing parts for both elements in figure 3C in position as preserved. The fragmentary malleus and ectotympanic of *Kryptobaatar* closely resemble the homologous bones in monotremes, in particular *Tachyglossus*. As discussed below, these similarities largely result from the retention of primitive mammalian features in both taxa.

The incomplete malleus probably preserves only the anterior process. In living mammals, the anterior process of the malleus

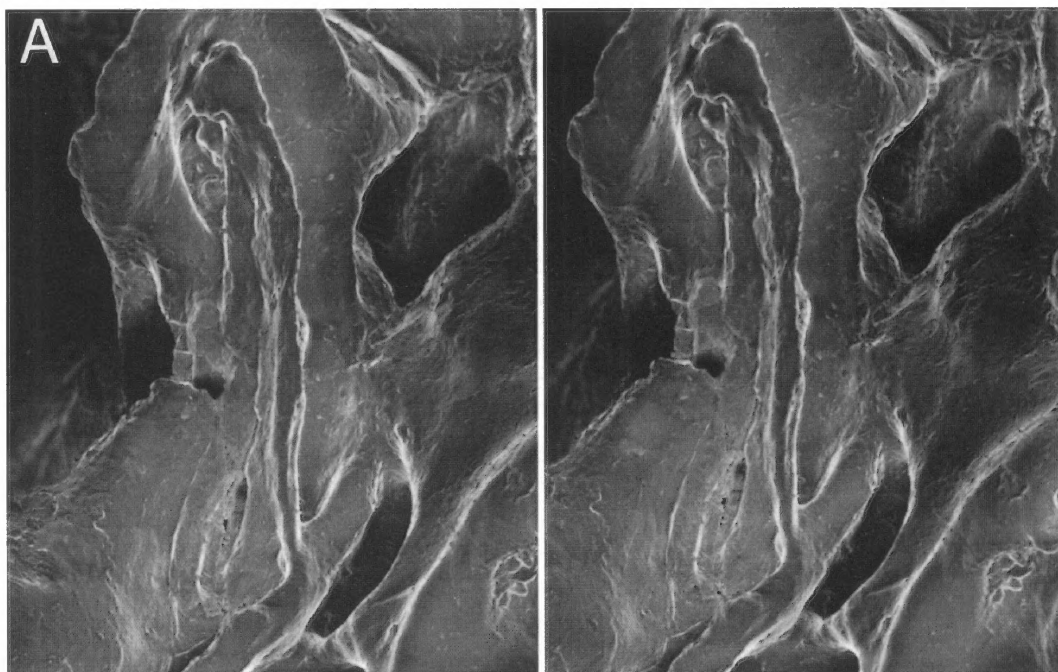


Fig. 3. Fragmentary right malleus and ectotympanic of *Kryptobaatar dashzevegi* PSS-MAE-113. **A**, SEM stereophotograph of elements as preserved in the epitympanic recess. **B**, Diagram of specimen shown in 3A. **C**, Hypothetical restoration of the malleus and ectotympanic oriented as in A and B. As discussed in the text, prior to fossilization these elements have been rotated along their main axis 90° or more from the presumed life position. Restoration of the malleus and ectotympanic is based on those of monotremes and generalized therians.

is formed by the goniale, a dermal element homologous with the prearticular; the goniale in turn is fused to the endochondral malleus, the homolog of the articular (Gaupp, 1913; Fleischer, 1973; Zeller, 1993). The foramen for the chorda tympani in living mammals lies either between these two elements or is wholly within the goniale (see Gaupp, 1913 for a full discussion of this matter). As we are unable to exclude the possibility of a contribution from the endochondral malleus in our specimen, we follow the literature of living mammals and describe the dermal goniale and endochondral malleus together under the term malleus.

Posteriorly, the element in question is more flangelike, and the malleus is the sole component. Anteriorly, the element is more rodlike, and both malleus and ectotympanic are present, though the malleus is only a thin apical lamina that abuts the medial surface of the ectotympanic. The suture demarcating

the malleus and ectotympanic is very distinct anteriorly and runs obliquely from the anteromedial to the posterolateral aspect of the rod. The suture disappears before reaching the posterolateral margin of the rod, where the two bones presumably are fused. Such fusion is also present in adult monotremes and presumably is primitive for Theria (Fleischer, 1978). The malleus is more robust posteriorly and is composed of two anteroposteriorly elongated laminae set at right angles to each other. The lamina on the exposed medial moiety is directed ventrally (our reconstruction suggests that in life this projection was dorsal); the lateral lamina is weaker, though its ventral edge is thickened, and lies in a plane parallel to the roof of the epitympanic recess. The junction of the two laminae is marked by an extensive sulcus. In life, the pars tensa of the tympanic membrane probably attached to the sulcus delimited by this ridge, as it does to a similar structure, the

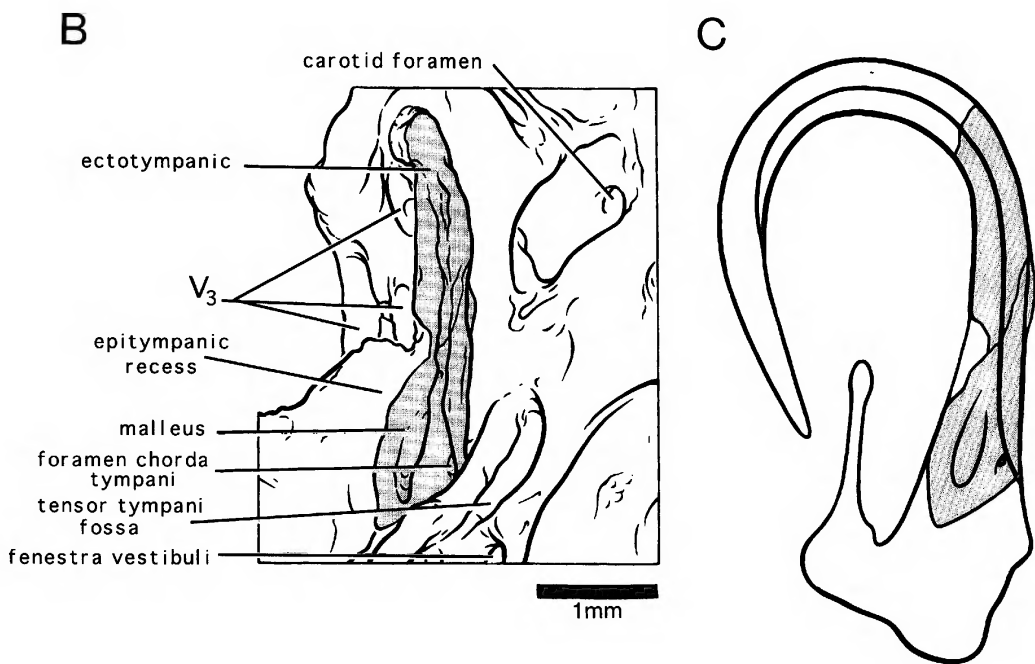


Fig. 3. Continued.

sulcus tympanicus, in living mammals. Medial to the sulcus tympanicus at the posterior end of the malleus is a shelflike surface that includes the small foramen for the chorda tympani discussed above. The posterior margin of the malleus is broken, and there is neither a manubrium nor an identifiable facet for articulation with the incus. If the foramen for the chorda tympani in PSS-MAE-113 has the same relative position as in living mammals, then the parts of the malleus that are missing include, in addition to the manubrium, a substantial portion posterior to the foramen, the pars transversalis (Fleischer, 1973). In living mammals, the foramen for the chorda tympani is placed well anterior to the pars transversalis, which connects the anterior process and the manubrium. The partial malleus of *Lambdopsalis* (Meng and Wyss, 1995) has a foramen for the chorda tympani situated well anterior to the incomplete pars transversalis.

As described above, the preserved segment of the ectotympanic in PSS-MAE-113 is intimately attached to the anterior process of the malleus. The most striking feature of the ectotympanic is the extensive sulcus tym-

panicus, continuous with the mallear part of this groove described above. On the lateral edge of the rod near its midpoint is a notch in the ectotympanic, which we believe is an artefact interrupting what would have been a continuous lamina. The rostral tip of the preserved portion of the ectotympanic shows an incomplete, laterally directed process, which in life was part of the ectotympanic rim.

The epitympanic recess is a deeply excavated, elongated, and ellipsoidal fossa (fig. 3A, B) trending roughly parallel to the long axis of the promontorium. This recess has contributions from three bones: the petrosal forms the bulk with the alisphenoid at the anteriormost end and the squamosal in the posterolateral corner. The posteromedial corner of the epitympanic recess shows an area more deeply excavated, the fossa incudis, which housed the crus breve of the incus in life. The medial wall of the fossa incudis is delimited by the prominent crista parotica and its rostral continuation, which forms a sharp, ventrally projecting crest (fig. 4). This crest forms a wall between the fossa incudis and the fenestra vestibuli (oval window) and

severely constrains the likely positions of the stapes and incus.

STAPES (FIG. 4)

On the left side of PSS-MAE-113, a small splint of bone is located on the anterodorsal rim of the fenestra vestibuli. This element has an approximate T shape. The medial end, which is partially inside the vestibule of the inner ear, corresponds to the top of the T; the lateral end, the vertical part of the T, is a long, bowed rod. If this bone is a fragment of a stapes, as interpreted here based on its size, position, and morphology, the lateral end is part of a crus and the medial end may be part of the footplate. Given the degree of bowing in the presumed crus, the stapes likely was stirrup shaped.

This interpretation is further supported by the presence of a well-developed vascular groove for the stapedia artery on the promontorium directed at the fenestra vestibuli and a foramen for one of the stapedia artery's end branches, the ramus superior (see Wible, 1987), located just anterolateral to the fenestra. The size and direction of the groove and the position of the foramen suggest that the stapedia artery ran across the fenestra vestibuli and through a stirrup-shaped stapes.

HYOID ELEMENTS

The skeleton of the hyoid arch in embryos of living mammals includes the stapes and Reichert's cartilage (Zeller, 1987; Novacek, 1993). The latter ossifies in the adult from as many as four independent centers to form a series of rod-shaped or columelliform elements not all of which are always present. The most proximal element, the tympanohyal, is fused to the crista parotica of the petrosal bone; the more distal elements, in order the stylohyal, epihyal, and ceratohyal, are part of the hyoid apparatus.

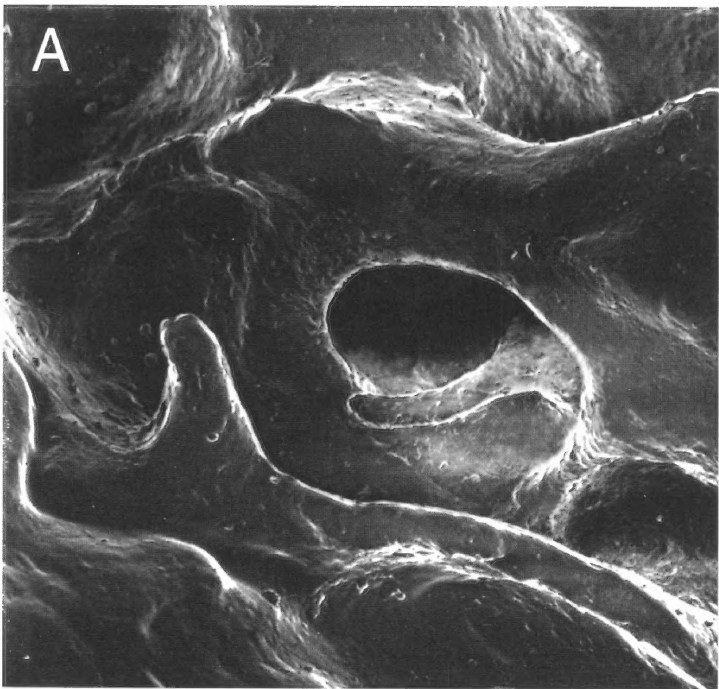
PSS-MAE-113 shows a slender fingerlike process extending ventrally from the crista parotica, more completely preserved on the left side, which we regard as the fused tym-

panohyal (fig. 4). In lateral view, the tympanohyal is triangular in outline; in ventral view, it is posteriorly and slightly medially directed, with a hooklike profile for cradling the hyomandibular branch of the facial nerve. As in living mammals, the facial nerve ran along the dorsomedial surface of the tympanohyal and left the middle-ear cavity posterior to it.

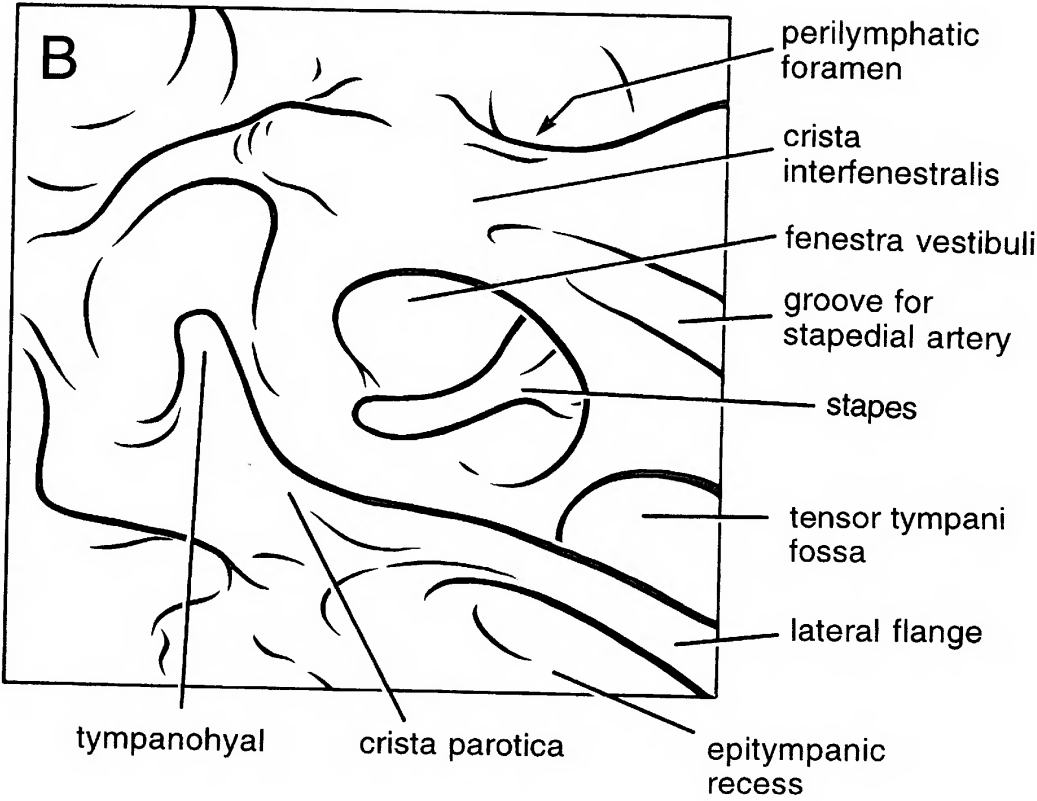
PSS-MAE-101 has no middle-ear ossicles preserved, but a long, slender, rod-shaped element is present on the right side, which we interpret as a stylohyal (fig. 2). From its posteriormost terminus, which is hidden by the paroccipital process, the stylohyal runs medially and then turns anteriorly toward the midline. It lies below and subparallel to the medial margin of the epitympanic recess. At its anterior end, the stylohyal is slightly dorsoventrally flattened and shows a broken surface. Thus, the full length of this element cannot be ascertained. As preserved, the stylohyal seems to have been displaced little from its life position; it may have been shifted slightly dorsally and posteriorly during preservation. Lying medial to the stylohyal is a fragment of a splintlike bone whose identity is uncertain. It is approximately of the same diameter as the stylohyal and may also be part of the skeleton of the hyoid arch.

The hyoid arch is closely related to the auditory bulla and tympanic cavity in various placentals (e.g., many lipotyphlans and macroscelidids; MacPhee, 1981). In fact, some portions of the hyoid are fused to the bulla or are connected to it through soft tissue. Allin and Hopson (1992) proposed that the hyoid arch gave support to the ectotympanic in the suspension of the ear ossicles. A more intimate role for the tympanohyal and stylohyal in basal mammaliaforms and non-mammalian cynodonts, that of providing posterior support to the tympanic membrane, was offered by Presley (1984a, b, 1993). He even envisioned a mechanism by which the tympanic membrane was tensed through the action of the levator hyoidei muscle on the

Fig. 4. Fragment of left stapes of *Kryptobaatar dashzevegi* PSS-MAE-113. **A**, SEM photograph, anteroventral oblique view of the element within fenestra vestibuli. **B**, Diagram of figure 4A.



1mm



hyoid. His proposal cannot be contradicted with fossil material (Novacek, 1993). Although Presley's model was elaborated for basal mammaliaforms and non-mammalian cynodonts, the position of the tympanohyal and the shape of the preserved segment of the stylohyal of *Kryptobaatar* suggest that the proximal segments of its hyoid arch were very close to the middle-ear bones. Restoring the hyoid arch to its presumed natural position in *Kryptobaatar* suggests that the proximal hyoid segments were intimately related to the tympanic cavity. Instead of supporting the tympanic membrane, the hyoid probably marked the ventralmost extension of the tympanic cavity and gave some support to the ectotympanic and to the membranous floor of the tympanic cavity that occurs, in the absence of an ossified bulla, in all extinct nontherian mammals.

DISCUSSION

The postdentary complex, quadrate, and fragmentary stapes are known in some Jurassic mammaliaforms (Kermack et al., 1973, 1981; Lillegraven and Krusat, 1991; Crompton and Luo, 1993). However, until recently, a single eutherian stapes was the only middle-ear ossicle known for a Mesozoic mammal (Archibald, 1979). Hurum et al. (1995) described an incus and fragmentary stapes and malleus for the multituberculate *Chulsanbaatar* from the Mongolian Late Cretaceous. Widely disparate hypotheses about the phylogenetic relationships of multituberculates have been proposed recently (cf. Kielan-Jaworowska, 1992; Kielan-Jaworowska and Gambaryan, 1994; Gambaryan and Kielan-Jaworowska, 1995; Sereno and McKenna, 1995; Wible et al., 1995), including one based on characters of the ear region (Meng and Wyss, 1995). Our specimens of *Kryptobaatar* provide new evidence bearing on the phylogenetic position of multituberculates, warranting a review of the characters from the auditory region employed in previous studies.

MULTITUBERCULATE EAR OSSICLES

Indisputable multituberculates are present in the fossil record from the Kimmeridgian?-Oxfordian to the Late Eocene (Hahn, 1969;

Krishtalka et al., 1982; Prothero and Swisher, 1992). A broken and heavily worn molar collected in a bonebed of Lower Rhaetian age in Belgium is purported to be the earliest record of multituberculates (Hahn et al., 1987). If it proves to be so, multituberculates have had a remarkable temporal range of slightly over 170 MY. To evaluate structure and diversity of the auditory region of this long-lived group, we have only fragmentary evidence available from three taxa: the Late Cretaceous *Chulsanbaatar* (Hurum et al., 1995) and *Kryptobaatar* (this paper) and the Late Paleocene taeniolabidid *Lambdopsalis* (Miao and Lillegraven, 1986; Miao, 1988; Meng, 1992; Meng and Wyss, 1995). Relying on such an incomplete record increases the risk of generalizations based on fragmentary material or on highly-specialized, atypical forms, such as *Lambdopsalis*. We critically review here the available evidence on multituberculate ear structure and compare it with the information derived from *Kryptobaatar*.

Lambdopsalis bulla

Eight specimens of *Lambdopsalis bulla* preserving one or more ear ossicles have been described to date. Miao and Lillegraven (1986) illustrated (fig. 5A) and briefly described a presumed malleus, incus, and stapes preserved essentially in situ on an isolated right petrosal (IVPP V7151.80); they also reported three other petrosals with partial stapes. In a subsequent restoration of the skull of *Lambdopsalis* by Miao (1988), the position of the three ossicles was altered slightly and a hypothetical ectotympanic was added. Meng (1992) described two stapes of *Lambdopsalis* recovered within the vestibule of the inner ear, which had been pushed through the fenestra vestibuli during fossilization. Finally, Meng and Wyss (1995) illustrated two specimens, one with a partial ectotympanic and malleus and the other with a partial malleus, and reconstructed the salient features of the ossicular chain. Their restoration (fig. 5C here) differed significantly from that of Miao and Lillegraven (1986) and Miao (1988), but no explanation for the differences was provided beyond suggesting

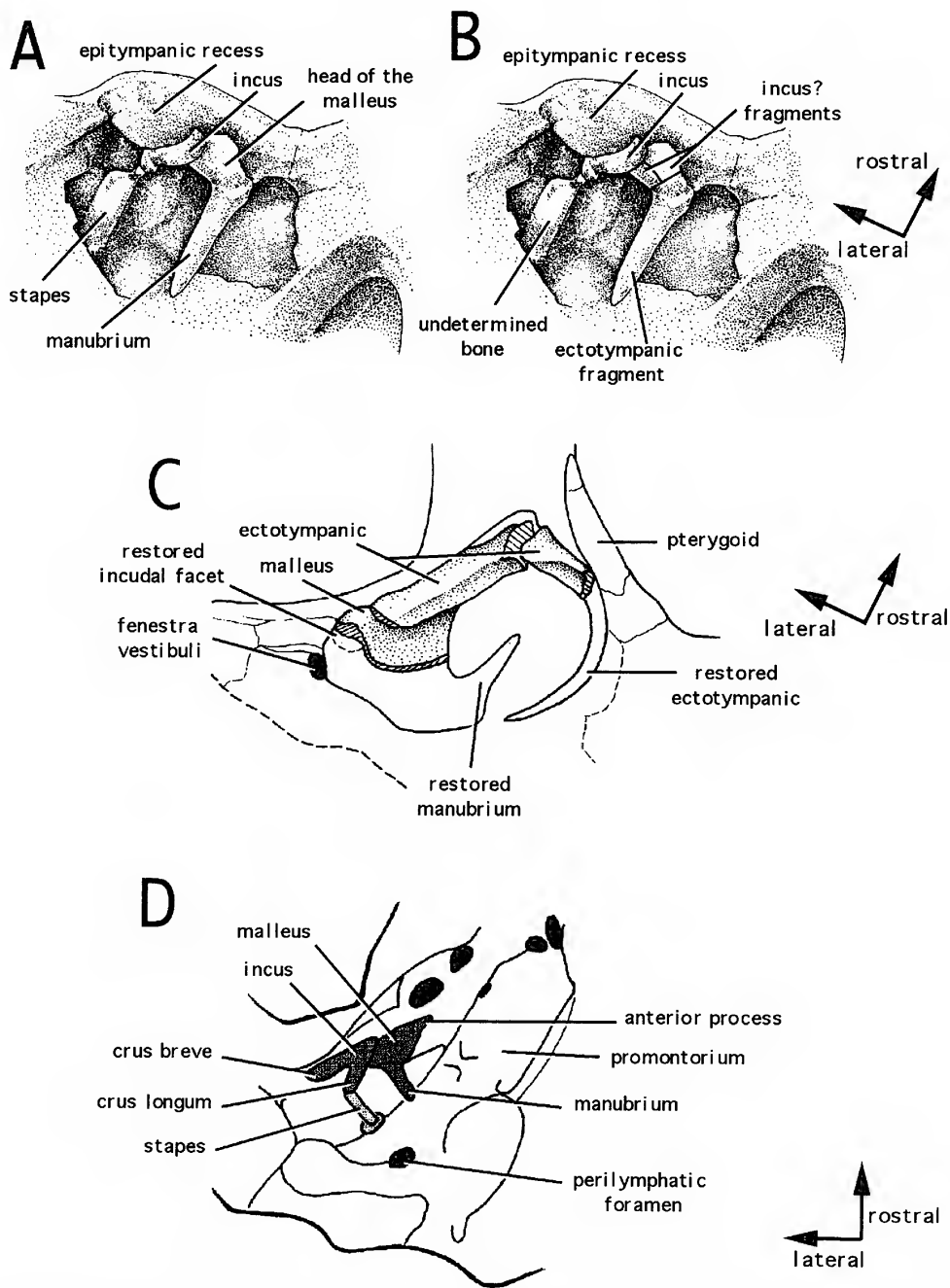


Fig. 5. Multituberculate ear ossicles in situ on the right side in ventral view. **A**, *Lambdopsalis bulla* IVPP V7151.80 as interpreted by Miao and Lillegraven (1986: fig. 1A). **B**, *L. bulla* IVPP V7151.80 as interpreted here (see text). **C**, *L. bulla* as restored by Meng and Wyss (1985: fig. 3b) based on IVPP V10777.1, V10777.2, and a photograph of V7151.80; redrawn and reversed from original figure. **D**, *Chulsanbaatar vulgaris* as restored by Hurum et al. (1995: fig. 1B) based on ZPAL MgM-I/86, I/108, and I/140; redrawn from original figure; stapedia footplate, manubrium, and anterior process of malleus are hypothetical. Figures are modified with permission or redrawn from the following sources: A, B, National Geographic Society (Miao and Lillegraven, 1986); C, Nature (Meng and Wyss, 1995); D, Hurum et al. (1995).

that the manubrium in IVPP V7151.80 had been displaced.

Lambdopsalis (IVPP V7151.80) provided the model not only for the restorations by Miao and Lillegraven (1986) and Miao (1988), but also for the restoration of the malleus in *Chulsanbaatar* by Hurum et al. (1995). Restudy of IVPP V7151.80 by one of us (JRW) reveals that the ossicles have been badly broken and displaced during fossilization and suggests that at least one element is not an ear ossicle. Two additional fragments of bone not described or illustrated by Miao and Lillegraven (1986) are located between the putative ossicular chain and the epitympanic recess, further indicating the degree of damage and displacement to which this specimen has been subjected. Additional preparation and full redescription of the ossicles in IVPP V7151.80 by A. R. Wyss and J. Meng is currently underway; the salient features of the various restorations of ear ossicles in *Lambdopsalis* are considered below.

Stapes. Two stapedial morphologies have been reported for *Lambdopsalis*. Meng (1992: fig 1) illustrated a nearly intact stapes with a distinct head that is deeply excavated anteriorly, a slender shaft perforated by a slit-like foramen, and an extensive, almost circular footplate. In contrast, the stapes figured by Miao and Lillegraven (1986: fig. 1A) is an imperforate, stout, rodlike element (fig. 5A). The footplate is not visible on the illustrated stapes.

Comparison of the stapedial shaft illustrated by Meng (1992) with that figured by Miao and Lillegraven (1986) reveals a substantial size discrepancy; the diameter in the former is approximately 0.25 mm, whereas it is about 0.75 mm in the latter. Reexamination of IVPP V7151.80 by JRW, the specimen of Miao and Lillegraven (1986), reveals that the stapes is, in fact, not a stapes. It is a robust, rodlike element broken at both ends, which bears no morphology indicative of an ear ossicle. Given its size, morphology, and preserved location, the stapes may be a displaced, damaged stylohyal or other element of the hyoid arch.

Incus. Miao and Lillegraven (1986: 501) reported that the only known incus of *Lambdopsalis* (fig. 5A) has a small but well-defined short process, a small body, shortened

long process, and a large lenticular process. From observations of their specimen by JRW, it is noted that what is described as the incudal body is dorsoventrally flattened. However, additionally, the incus may be a larger element than originally interpreted. The malleus of these authors is composed of at least three broken pieces (fig. 5B). The one labeled manubrium by Miao and Lillegraven (fig. 5A) will be discussed separately below under the ectotympanic. The other two, which form the so-called mallear head (fig. 5A), are laminar and appear to be continuous with the incus described by Miao and Lillegraven. Given this apparent continuity, it is possible that one or both of these elements are part of the incus. If this is not the case, we see no compelling evidence to identify them as part of the malleus or any other ear ossicle. In any event, the situation is highly ambiguous.

Given that the morphology of the only known incus of *Lambdopsalis* is unsettled, the arrangement of the articular surface for the malleus on the incus is also uncertain. Miao and Lillegraven (1986: 501) claimed that the articulation is long and flat, and as illustrated in their figure 1A (fig. 5A here), the mallear head appears to lie anterior (and medial) to the incudal body, as in therians. In contrast, Meng and Wyss (1995) reconstructed the incus dorsal to the malleus (fig. 5C), identifying a fossa on the posterodorsal surface of the broken mallear body as for the incudal articulation. A predominantly dorsoventral incudomallear articulation is present among living mammals only in monotremes.

Both reconstructions of the incudomallear articulation present problems. As pointed out above, we believe that the mallear head is misidentified in the model by Miao and Lillegraven (1986) and, therefore, the incudomallear articulation is not preserved essentially in situ. With regard to Meng and Wyss (1995), until a full description of their specimen (IVPP V10777.1) is completed, it is unclear what surface of the only known incus of *Lambdopsalis* articulated with the so-called incudal fossa on the posterodorsal surface of the malleus. Consequently, the true nature of the incudomallear articulation remains ambiguous.

Malleus. Two malleal morphologies have been reported for *Lambdopsalis*. Problems concerning the malleus described by Miao and Lillegraven (1986) have been treated above and will be continued under the ectotympanic. The more complete of the two partial mallei described by Meng and Wyss (1995) preserves a very long, robust anterior process connected to the ectotympanic and an incomplete, broad body (pars transversalis). The second partial malleus shows a foramen for the chorda tympani nerve on the dorsal surface of its robust anterior process. A manubrium is not preserved in either malleus described by Meng and Wyss (1995), but a hypothetical one is reconstructed as short, thin, and anteromedially directed (fig. 5C). The basic facts of their interpretation of the malleus are congruent with ours for *Kryptobaatar*.

Ectotympanic. Miao (1988: fig. 26) restored the ectotympanic and the anterior process of the malleus of *Lambdopsalis* as of the free mobile type of Fleischer (1978), but explicitly stated that these elements were conjectural; therefore, his restoration will not be discussed further. Meng and Wyss (1995) have described two well-preserved fragments of an ectotympanic in *Lambdopsalis* (IVPP V10777.1). The most striking feature of both fragments is a broad and deep sulcus tympanicus delimited by two crests, as occurs in *Kryptobaatar*, monotremes, and basal therians. In addition, Meng and Wyss (1995) reported that the ectotympanic lies nearly horizontal and is in contact with the pterygoid (fig. 5C). Whereas an essentially horizontal position for the ectotympanic seems likely, the contact of this element with the pterygoid is in our opinion an artefact. The purported contact is between the pterygoid's hamular process and the smaller fragment of the ectotympanic. We note that both of these are broken elements. A large crack (noted by Rougier et al., 1996, and visible in Meng and Wyss, 1995: fig. 1b) separates the hamular process from the skull base (contra Meng and Wyss, 1996), and the ectotympanic fragment is separated from the larger portion of that bone by a wide gap. Furthermore, the difference in the orientation of the two broken pieces of the ectotympanic reveals that the smaller fragment is not in its natural position,

but has shifted anterodorsally to make contact with the pterygoid. When the smaller fragment, which is preserved in a near horizontal position, is brought into proper alignment, it assumes a more inclined position, producing a sizable gap between the ectotympanic and pterygoid.

When the ectotympanic of Meng and Wyss (1995) is compared with that of monotremes and with the putative ossicular chain of Miao and Lillegraven (1986), it is clear that the so-called manubrium in IVPP V7151.80 is in fact a distal portion of the ectotympanic (fig. 5B). As mentioned above, the malleus of Miao and Lillegraven is composed of three fragments: the two laminar pieces already described in conjunction with the incus and the manubrium. The last exhibits a different orientation from and has no structural continuity with the former two, being separated from them by a layer of sediment. Other than its long and gracile morphology, the manubrium shows no distinctive features characteristic of mammalian manubria. It lacks a broad, flattened tip for the attachment of the tympanic membrane, as occurs in living mammals. Moreover, like the ectotympanic of Meng and Wyss (1995), the manubrium is essentially U shaped in cross section, with a deep furrow demarcated by well-developed crests, noted in the original description by Miao and Lillegraven (1986) but not visible in their figure 1A. Manubria vary considerably in living mammals, but none possesses such a deep furrow (Doran, 1878; Henson, 1961; Fleischer, 1973). Furthermore, it is difficult to envision a functional correlate for a furrow on the manubrium. In contrast, the sulcus tympanicus of the ectotympanic provides attachment for the tympanic membrane.

The manubrium of Miao and Lillegraven (1986) is of an appropriate size to be part of an ectotympanic, such as the partial one described by Meng and Wyss (1995). The length of the manubrium is about 3 mm, whereas the element of Meng and Wyss, which includes part of the malleus in addition to the ectotympanic, is about 5 mm long. Additionally, the length of the manubrium of Miao and Lillegraven (1986) in proportion to the malleal body seems excessive, especially

compared with the proportion of these same elements in monotremes.

Chulsanbaatar vulgaris

Hurum et al. (1995) described fragmentary ossicles on skulls of the Late Cretaceous *Chulsanbaatar*, which is thought to be a more generalized form than *Lambdopsalis*. Specimens exhibiting a stapedial shaft associated with an almost complete incus (ZPAL MgM-I/108), two partial incudes (ZPAL MgM-I/140), and a part of an incus and a possible fragment of malleus (ZPAL MgM-I/86) were included. Also presented was a restoration of the ear ossicles in *Chulsanbaatar*, reproduced as figure 5D here, based largely on the restoration by Miao and Lillegraven (1986) and Miao (1988). Hurum et al. (1996) no longer support this reconstruction, and we await publication of their redescription of these specimens with updated interpretations.

Stapes. The stapedial shaft identified by Hurum et al. (1995) is rodlike and has been displaced laterally from the fenestra vestibuli. Restudy of the specimen by one of us (GWR) after additional preparation reveals that the shaft is broken at both ends and curved slightly posteriorly. Because such curvature is an unusual feature for the shaft of a mammalian stapes, we are uncertain of the true nature of this element—whether it is a stapedial shaft, a stapedial crus, a hyoid element, or other bone fragment. Until additional material is found, we prefer to consider the stapedial morphology of *Chulsanbaatar* as uncertain.

Incus. Four fragments of incudes are reported by Hurum et al. (1995), each found preserved within the epitympanic recess, although the orientation was not identical in all specimens. As described and illustrated by Hurum et al. (1995), the incus is in general a simple and flat bone exhibiting a peculiar A or boomerang shape with the body at the apex and a notch that faces posterolaterally and delimits two legs; the lateral one, the crus breve, is longer and more robust than the medial, the crus longum (fig. 5D).

After restudy of these incudes by GWR, we are uncertain as to the extent of damage to any of the four. One of the reviewers of

an earlier version of our paper, R. Presley, also an author of Hurum et al. (1995), pointed out in his review that he currently believes that the crus longum as preserved is incomplete in *Chulsanbaatar*. In Hurum et al.'s (1995) restoration of the ossicular chain (fig. 5D), the incus lies posterolateral to the malleus, which closely resembles the incudomalleolar articulation illustrated for *Lambdopsalis* by Miao and Lillegraven (1986).

The position of the incus in life in *Chulsanbaatar*, as in *Kryptobaatar* and other Late Cretaceous Mongolian multituberculates, is constrained by the well-developed, ventrally projecting crista parotica and medial wall of the epitympanic recess (visible in Kielan-Jaworowska et al., 1986: fig. 14A), although variation in the development of this crest has been noted (Hurum et al., 1995). In order to articulate the crus breve in the fossa incudis and the crus longum with the stapes, the flat incus must have had an inclined orientation (Hurum et al., 1995).

The interpretation of the incus of *Chulsanbaatar* by Hurum et al. (1995) differs in some regards from that of *Lambdopsalis* by Miao and Lillegraven (1986). In *Chulsanbaatar*, a lenticular process is apparently lacking and the crus breve is well developed, being longer and more robust than the crus longum (fig. 5D). In contrast, in *Lambdopsalis*, a distinct neck and a large lenticular process are present, the latter presumably articulates with a corresponding depression on the stapedial head (Meng, 1992), and the crus breve is extremely short and blunt (fig. 5A). We are uncertain of the meaning of these differences. However, a close comparison of the taxa is hampered by the poor preservation of all the elements in question.

Malleus. Hurum et al. (1995) found a fragment of bone in the anterior part of the epitympanic recess, which they claimed was best interpreted as the head of the malleus (fig. 5D). They further speculated that the manubrium, when restored, must have had a vertical component to its orientation given the vertical slope of the epitympanic recess. Restudy of the specimen by GWR reveals the fragment to be similar in size to the preserved partial incus and without distinguishing features. This may be part of the malleus,

but we see no basis for identifying it as the malleal head.

Hyoid. Kielan-Jaworowska and Gambaryan (1994: fig. 19) described a fragmentary hyoid apparatus in *Chulsanbaatar*. The rod-like elements were interpreted as stylohyoids (stylohyals), but the curvature of these bones renders this interpretation unlikely. These elements are convex dorsally, whereas in living mammals and in *Kryptobaatar* the stylohyals are concave dorsally. In addition, these elements were preserved well away from the mandible, suggesting that they may be part of the first cornu branchiale.

Ectypodus tardus

An ectotympanic was figured for the Early Eocene ptilodontoid *Ectypodus tardus* (YPM-PU 14724) by Sloan (1979: fig. 1). After restudy of this element, we do not consider it to be an ectotympanic, because it is too small and shows no conspicuous ectotympanic features. In fact, it appears to be the ventral tip of the broken paroccipital process.

Summary of Multituberculate Ear Ossicles

Our present knowledge of multituberculate ear ossicles can be summarized as follows. Three different stapedial morphologies have been proposed: (1) slender, columelliform with a stapedial slit (Meng, 1992); (2) sturdy, rodlike (Miao and Lillegraven, 1986; Hurum et al., 1995); and (3) bicurrate (this paper). Only Meng's (1992) columelliform element in *Lambdopsalis* is unquestionably a stapes. The element described here in *Kryptobaatar* is probably a bicurrate stapes. The rodlike element of Hurum et al. (1995) is suspect, whereas that of Miao and Lillegraven (1986) is certainly not a stapes. The multituberculate incus is a flat element with two proposed morphologies: (1) an A-shaped bone with a body at the top of the A, the crus breve more robust and perhaps longer than the crus longum, and no differentiated structure for the stapedial articulation (Hurum et al., 1995); and (2) a small body with a prominent lenticular process at the end of the well-developed crus longum and a small, blunt crus breve (Miao and Lillegraven, 1986). The full

morphology of the incus is uncertain in either instance, as are the shape and orientation of the incudomalleal articulation. Two morphologies have been proposed for the multituberculate malleus: (1) a large anterior process that is strongly attached or partially fused to the ectotympanic and with an internal sulcus that is continuous with the sulcus tympanicus of the ectotympanic, a large pars transversalis, and no protruding head, with the manubrium unknown (Meng and Wyss, 1995; this report); and (2) a well-developed head, a robust, long manubrium that is directed posteriorly or posteromedially and has a deep furrow, and the anterior process unknown (Miao and Lillegraven, 1986; Miao, 1988). Of these two malleal morphologies, we believe the former to be correctly identified. The manubrium in the latter is actually part of the ectotympanic, and the head consists of two fragments that may eventually be related to the incus or be wholly unrelated to the ossicular chain. The only taxa for which the ectotympanic is known, *Lambdopsalis* and *Kryptobaatar*, have this element strongly attached (or partially fused) to the anterior process of the malleus, with a deep sulcus tympanicus continuous with that of the malleus. In *Lambdopsalis*, the preserved ectotympanic fragments suggest a degree of inclination similar to that in *Tachyglossus*, which is roughly 25 to 30° from the horizontal. Given that the preserved portion in *Kryptobaatar* is displaced, the ectotympanic inclination is not known.

COMPARISONS WITH MONOTREMES

Among living mammals, monotreme ossicles resemble those known for multituberculates. They have in common a massive anterior process of the malleus that is partially fused with or strongly attached to the ectotympanic, and a large pars transversalis (body) of the malleus. Given that these features also occur in primitive marsupials and placentals (Doran, 1878; Fleischer, 1973), they are likely to be primitive for mammals. Other shared ossicular resemblances, however, have been considered to be synapomorphies of monotremes and multituberculates. Included are the columelliform stapes (Meng, 1992), the flat shape of the incus and

its dorsal position with respect to the malleus, the contact between the ectotympanic and the pterygoid, and the horizontal position of the ectotympanic (Meng and Wyss, 1995). These characters already have been critiqued in a brief communication (Rougier et al., 1996), but are reviewed more thoroughly in the following. A phylogenetic analysis to determine whether these characters represent synapomorphies of monotremes and multituberculate is presented separately below.

Columelliform Stapes

Meng (1992) proposed that a columelliform stapes and an extrastapedial course for the stapedial artery are monotreme/multituberculate synapomorphies. Supporting this view was the similar stapedial morphologies in *Lambdopsalis* and living monotremes; indeed, the only apparent distinctions between these forms are the presence in *Lambdopsalis* of a minute foramen in the stapedial shaft and a deeply excavated articular surface on the head. Additionally, an extrastapedial course for the stapedial artery occurs in the platypus (Wible, 1987) and is indicated by a groove for the stapedial artery running behind the fenestra vestibuli in *Lambdopsalis* (Miao, 1988). Also supporting Meng's view is the fragmentary columelliform stapes described in *Chulsanbaatar* by Hurum et al. (1995), although we have expressed doubts about the true nature of this element (see above).

Whereas monotremes and *Lambdopsalis* have remarkably similar stapes, they are not the only mammals to have this morphology. Columelliform stapes are also found in pholidotans and many marsupials, and in fact may be primitive for Marsupialia (Novacek and Wyss, 1986; Gaudin et al., 1996). Additionally, other evidence indicates that a columelliform stapes and an extrastapedial course for the stapedial artery are not the only conditions in multituberculates. Several authors (Rougier et al., 1992; Rougier, 1993; Wible and Hopson, 1995) have proposed that at least in some Late Cretaceous multituberculates a sizable stapedial artery ran across the fenestra vestibuli, through a bicurrate stapes, based on the presence of a groove on the promontorium notching the oval window.

In addition, we have argued here that *Kryptobaatar* likely had a bicurrate stapes. It also had a stapedial artery, given the presence of a groove on the promontorium and of a foramen for one of the stapedial artery's end branches, the ramus superior. The groove on the promontorium in *Kryptobaatar* does not extend to and notch the fenestra vestibuli as it does in some other Late Cretaceous multituberculates. However, reconstruction of a stapedial artery passing through the bicurrate stapes in *Kryptobaatar* is justified, because in living mammals with both a bicurrate stapes and a stapedial artery, the artery invariably passes through the stapedial foramen (Tandler, 1899; Bugge, 1974; Wible, 1987).

For the phylogenetic analysis conducted below, we employ three characters of the stapes, which account for the presence of a head, the position of the crus/crura, and the size of the stapedial foramen (appendix 1: 52–54). Stapes have not been recovered for many extinct mammalian taxa. The incudal end is known only in the tritheledontid *Pachygenelus* (Allin and Hopson, 1992) and in *Sinoconodon* (Meng, 1992; Crompton and Luo, 1993); both stapes are bicurrate and with a broad distal end articulating with the quadrate, also the condition in non-mammalian cynodonts (e.g., *Thrinaxodon*, Estes, 1961; *Exaeretodon*, Bonaparte, 1966). In contrast, a stapedial head, a constricted distal end set off by a neck, occurs in *Lambdopsalis*, monotremes, marsupials, and eutherians. Regarding the position of the crus/crura, we recognize four states: (1) the crura are parallel and positioned at the margin of the footplate in *Pachygenelus* (Allin and Hopson, 1992), as in *Thrinaxodon* (Estes, 1961) and *Exaeretodon* (Bonaparte, 1966); (2) the crura are parallel with the posterior one at the edge of the footplate, but the anterior one is recessed in from the edge in the Jurassic mammaliaforms *Morganucodon* (Kermack et al., 1981) and *Haldanodon* (Lillegraven and Krusat, 1991); (3) the crura converge, forming a triangular stapes in most therians (Doran, 1878; Fleischer, 1973; Gaudin et al., 1996); and (4) only a single crus is present in *Lambdopsalis*, monotremes, and some therians. A stapes is not preserved for the prototribosphenidan *Vincelestes*, but it was likely bicurrate given that the groove on the

promontorium for the stapedial artery notches the fenestra vestibuli (Rougier et al., 1992). Finally, it is uncertain which of the bicurrate states is present in *Kryptobaatar*, as the footplate is not preserved. Regarding the size of the stapedial foramen, following Gaudin et al. (1996), we recognize three states: (1) well developed; (2) microperforate; and (3) absent.

We do not include a character for the course of the stapedial artery in our analysis. The presence of this artery in extinct taxa can only be deduced unequivocally from a groove on the cochlear housing directed towards the fenestra vestibuli (Wible, 1987), which is dependent on the state of preservation. In our analysis, the only taxa with such a groove are *Vincelestes* and perhaps *Placentalia* (Gaudin et al., 1996). Whereas a groove is found in some Late Cretaceous and Cenozoic multituberculates, it is absent in the Late Jurassic paulchoffatiids (Hahn, 1988; Lillegraven and Hahn, 1993).

Shape and Position of the Incus

Meng and Wyss (1995) proposed that a simple, flat incus positioned dorsal to the malleus is a monotreme/multituberculate synapomorphy. Following these authors, separate characters for the shape and for the position of the incus (quadrate) are included in our phylogenetic analysis (appendix 1: 55, 56) and are discussed individually below.

Whereas the shape of the incus varies widely among living mammals (Doran, 1878; Fleischer, 1973), that of monotremes displays a very conspicuous morphology. Their incus is a small, very flat bone with a subtriangular shape (Kuhn, 1971; Fleischer, 1973; Zeller, 1993). The multituberculates *Lambdopsalis* and *Chulsanbaatar* also have an incus with a flattened body, though not to the same extent as in monotremes, which is unlike the complex form of the quadrate known for non-mammalian cynodonts (Luo and Crompton, 1994) and the incus of therians (Fleischer, 1973). The simple form of the incus in monotremes and multituberculates does not afford a wealth of comparisons, but it is reasonable to regard a simple incus with a flattened body as a derived fea-

ture occurring in monotremes and multituberculates.

Zeller (1993) observed two types of incudomalleolar articulation among living mammals; the incus is positioned posterior to the malleus in therians and is medial (dorsal) in monotremes. He proposed that the latter is the derived condition, but offered no rationale for this. The incus is affixed dorsally to the malleus in adult monotremes (Kuhn, 1971; Fleischer, 1973). In fact, in ventral view, the incus is covered almost completely by the malleus; only the tip of the crus breve is exposed and via this surface the ossicular chain is anchored to the skull in the fossa incudis. Based on a monotreme model, Meng and Wyss (1995) interpreted a fossa on the dorsal surface of the malleus in *Lambdopsalis* as articulating with the incus (fig. 5C). In addition, they treated the dorsally positioned incus of monotremes and *Lambdopsalis* as synapomorphous, noting that the incudomalleolar (quadrate-articular) articulation is anteroposterior in non-mammalian cynodonts as well as in therians.

To begin, the position of the incudomalleolar articulation in therians requires clarification. The incus does lie posterior to the malleus in therians, but in many instances part of the malleus also extends dorsal to the incus (see Fleischer, 1978). However, it is accepted here that the main articulation, the center of mass, is in an anteroposterior orientation in therians.

Two questions are raised by Meng and Wyss's (1995) claim: first, does any multituberculate have an incus lying dorsal to the malleus, and second, do non-mammalian cynodonts have a predominantly anteroposterior articulation between the quadrate and articular? As discussed above, the exact positional relationship between incus and malleus in multituberculates is uncertain. Additionally, an anteroposterior articulation between the quadrate and articular does not reflect the position of these elements in all non-mammalian cynodonts. Whereas the major orientation appears to be anteroposterior in the mammaliaforms *Morganucodon* (Kermack et al., 1973, 1981), *Megazostrodon* (Gow, 1986), and *Haldanodon* (Lillegraven and Krusat, 1991), it differs in non-mammaliaform cynodonts (Crompton, 1972). The

quadrate in the last forms appears to lie chiefly posterior to the articular (Sues, 1986: fig. 15), but in fact the quadrate facet on the articular is prolonged posteriorly onto a well-developed horizontal shelf (Sues, 1986: fig. 16A), which gives the articulation an orientation intermediate between anteroposterior and dorsoventral. This horizontal shelf is not found on the mammaliaform articular. Nevertheless, we code the incudomalleolar articulation as a binary character here, with the certainly derived dorsoventral articulation as one state and the predominantly anteroposterior and intermediate conditions subsumed under the primitive state.

Two other characters of the quadrate (incus) are included in our phylogenetic analysis (appendix 1: 57, 58). The first of these, taken from Meng and Wyss (1995), concerns the load-bearing properties of the quadrate. According to these authors (p. 143), the quadrate (incus) is reduced, losing the occlusal force from masticatory movement of the mandible in multituberculates, monotremes, marsupials, and placentals; in contrast, in the outgroups to these taxa, the quadrate bears loads transmitted through the lower jaw. This character is difficult to code, because whether or not the quadrate is load-bearing cannot be determined without knowing how the masticatory forces are balanced around the jaw joint. In fact, Crompton and Hylander (1986) hypothesized that the quadrate did not carry any load from masticatory movement in basal mammaliaforms. However, in order to be as close as possible to Meng and Wyss's (1995) data, we retain this character and modify its description to account for differences in the relative size of the quadrate's articulation with the skull base. The second character concerns the shape of the quadrate (incus) articulation with the articular (malleus). In the mammalian outgroups, this articulation is strongly convex (Luo and Crompton, 1994), but it is much flatter in mammals (Fleischer, 1973).

Ectotympanic-Pterygoid Contact

Meng and Wyss (1995) proposed that contact between the ectotympanic and pterygoid is a monotreme/multituberculate synapomorphy. Given that the ectotympanic (angular) is

part of the lower jaw and not suspended from the skull in non-mammalian cynodonts, contact between the ectotympanic and any skull element would be a derived feature. However, the character of ectotympanic-ptyergoid contact is not included in our phylogenetic analysis for reasons enumerated below.

The first issue is whether or not the ectotympanic contacts the pterygoid in multituberculates. As detailed above, in the only specimen allegedly showing an ectotympanic-ptyergoid contact (fig. 5C), i.e., *Lambdopsalis* IVPP V10777.1, both the ectotympanic and the pterygoid are broken. Moreover, our interpretation of the two preserved, broken pieces of the ectotympanic would, upon restoration to the natural position, move the element ventrally away from contact with the pterygoid, leaving the ectotympanic merely in close proximity to the pterygoid, as occurs in many living placentals (e.g., lipotyphlans) and in the purported basal placentals *Asiorcytes* and *Kennalestes* (Kielan-Jaworowska, 1981). Consequently, we consider the contact between the ectotympanic and pterygoid shown in *Lambdopsalis* (IVPP V10777.1) to be an artefact.

Secondly, does the ectotympanic contact the pterygoid in monotremes? To address this, we discuss the three genera of extant monotremes separately. In juvenile *Tachyglossus*, the ectotympanic and the anterior process of the malleus are strongly attached to an independent dermal ossification positioned ventral to the pterygoid known as the echidna pterygoid and to the raised posterior region of the promontorium, which form the anteromedial and posterior margins of the tympanic cavity, respectively (Kuhn, 1971; Wible and Hopson, 1995: fig. 3). This produces a middle-ear space fairly enclosed by bone. The echidna pterygoid is thought to be homologous with the ventral pterygoid of the compound pterygoid of embryonic therians, which becomes the hamulus in the adult (Presley and Steel, 1978; Moore, 1981). In older *Tachyglossus*, the ear ossicles are not as extensively connected with the echidna pterygoid. The anterior process of the malleus retains a conspicuous process that meets a small facet in the anterolateral surface of the echidna pterygoid. However, the ectotympanic may contact the echidna pterygoid

(e.g., AMNH 105202, 105975) or may be merely anchored through connective tissue to it (e.g., AMNH 154459, 107185). In adult *Zaglossus*, the borders of the middle-ear space are produced by the same bony elements as in *Tachyglossus*. The major exception is that the anterior process of the malleus is not attached to the echidna pterygoid, but to an area lateral to it, which in *Tachyglossus* is known to be formed by the ossification within the sphenoobturator membrane (Kuhn, 1971; Kuhn and Zeller, 1987). The ectotympanic may (e.g., AMNH 17231) or may not (e.g., AMNH 194702, 157072) contact the echidna pterygoid.

In contrast to tachyglossids, in young and adult *Ornithorhynchus*, the ectotympanic is supported only through connective tissue (Gates et al., 1974; Zeller, 1989): the ossicular chain is not firmly anchored to bony structures but floats in a cavity surrounded by connective tissue and muscle (Gates et al., 1974: 155). The ectotympanic approaches and is held by connective tissue to the echidna pterygoid, which is a weak laminar element without any facet for the articulation of either the ectotympanic or the malleus. In fact, because the ectotympanic of the platypus is a vibrational element moving in concert with the malleus (Gates et al., 1974), the absence of ectotympanic-skull contact is essential. Also, in contrast to tachyglossids, the middle-ear space of *Ornithorhynchus* as well as that of the Miocene platypus *Obdurodon* (Archer et al., 1993) is not delimited by surrounding bony processes.

We consider the contact between the ectotympanic and the echidna pterygoid (the pterygoid of Meng and Wyss, 1995) exhibited by some tachyglossids to be a unique feature of these forms and, therefore, exclude this character from our phylogenetic analysis. When comparing monotremes with other mammalian morphs, the condition of the palate and ear region in ornithorhynchids appears to be more generalized than that of tachyglossids. As occurs in some other ant- and termite-eaters (e.g., myrmecophagids), the hard palate is prolonged posteriorly between the right and left ear regions in tachyglossids. What distinguishes the expanded tachyglossid palate from that of other ant- and termite-eaters is that the posterolateral part is com-

posed of an enlarged echidna pterygoid, which as an independent ossification is unique to monotremes among mammalian morphs (Miao, 1988; Wible, 1991). The expansion of the palate brings the echidna pterygoid in tachyglossids into close proximity to, and in some cases contact with, the ectotympanic. According to Griffiths (1968), the expanded palate increases the surface area upon which the echidna grinds its food, between keratinous spines on the mucosa of the tongue and the palate. Not only is the arrangement of the palate in tachyglossids unique, but a middle-ear space delimited by bony processes along the medial and posterior margins is also very unusual among mammalian morphs; a similar or greater degree of enclosure is found only among therians. Perhaps middle-ear enclosure in tachyglossids protects that space from the grinding action taking place on the palate. In contrast to the condition in tachyglossids, a well-developed medial tympanic wall is lacking in ornithorhynchids and in other non-therian mammalian morphs. Moreover, a vibrational ectotympanic-malleus complex as in *Ornithorhynchus* is presumed to be the condition in those mammalian morphs in which the postdentary bones had been released partially or completely from the lower jaw (Allin, 1975; Allin and Hopson, 1992).

Horizontal Position of the Ectotympanic

Meng and Wyss (1995) proposed that the horizontally positioned ectotympanic (and malleus) occurring in *Lambdopsalis*, *Ornithorhynchus*, and tachyglossids represents a synapomorphy of multituberculates and monotremes, with the plesiomorphic condition present in near outgroups such as *Morganucodon* being a relatively vertical angular. Additionally, following Zeller (1993), they postulated that the horizontal ectotympanic found in some therians is convergently acquired.

In evaluating this character, the first issue is whether or not the ectotympanic in monotremes and *Lambdopsalis* is horizontally positioned. In his description of *Ornithorhynchus*, Zeller (1993) observed that the ectotympanic is not strictly horizontal, but is

inclined at 25 to 30° from the horizontal. We have seen a similar degree of inclination in tachyglossids. Regarding *Lambdopsalis*, as stated above, we repeat that reconstructing the precise posture of the ectotympanic in *Lambdopsalis* is difficult because that bone is broken and displaced (fig. 5C); it is not preserved in original life position as was claimed by Meng and Wyss (1995). Nevertheless, we accept that the ectotympanic is inclined at an angle similar to that in monotremes, roughly 25 to 30°, a condition that we deduce both from the preserved fragments of malleus and ectotympanic and from the orientation of the fenestra vestibuli documented by Meng and Wyss (1996). Given that the ectotympanic inclination in monotremes and *Lambdopsalis* is not strictly horizontal, we call this condition near-horizontal. We further caution that no living mammal has a truly horizontal ectotympanic (Klaauw, 1931) and that character state as used by Meng and Wyss (1995) includes ectotympanics inclined up to 30°.

The second issue concerns the condition in other taxa. In coding the inclination of the ectotympanic (angular) in mammals and their near outgroups, Wible (1991) identified three states: vertical, roughly horizontal, and inclined. He reported the angular to be vertical in all mammaliaforms with postdentary bones attached to the jaw, roughly horizontal in monotremes, and inclined in multituberculates, marsupials, and placentals. At the time, an ectotympanic was not known for any multituberculate (except *Ectypodus*, see above). Wible (1991) used the orientation of the fenestra vestibuli to approximate the orientation of the ectotympanic in multituberculates, following Allin (personal commun. to Wible, 1991; Allin and Hopson, 1992) who noted that the tympanic membrane lies essentially parallel to the plane of the fenestra vestibuli in generalized living mammals. Using this model, an inclined ectotympanic was postulated for multituberculates based on the inclined fenestra vestibuli in Late Jurassic paulchoffatiids and Late Cretaceous cimolodonts.

In reevaluating this character here, we reiterate that the angular is positioned close to the vertical in non-mammalian cynodonts (Allin, 1975, 1986; Allin and Hopson, 1992).

However, we are less convinced that we can distinguish a highly inclined ectotympanic from the vertical or one with a low inclination from near-horizontal (up to 30°). Therefore, in coding this character (appendix 1: 59), we modify it to a binary one with the certainly derived near-horizontal condition as one state and the vertical and inclined conditions subsumed under the primitive state (see discussion of the coding for this character in various taxa below).

In scoring those taxa for which the ectotympanic (angular) is not known, we rely on Allin's proposal that the orientation of the fenestra vestibuli approximates that of the ectotympanic. Meng and Wyss (1996) have rejected Allin's proposal, stating that it is too often contradicted. As examples, they offered *Lambdopsalis* in which a supposed horizontal ectotympanic occurs with an oval window inclined approximately 30°, *Morganucodon* in which a vertical angular occurs with an inclined oval window, and *Scutisorex* (AMNH 48474) in which a supposed horizontal ectotympanic occurs with an antero-ventrolateral oval window. Rather than contradicting Allin's proposal, we believe these instances are congruent with it, but suffer from the ambiguous use of the terms horizontal and inclined by Meng and Wyss. As stated above, we accept that the ectotympanic in *Lambdopsalis* is inclined as in monotremes, approximately 25 to 30°, which is congruent with the inclination of the oval window reported by Meng and Wyss (1996). Regarding *Morganucodon*, Meng and Wyss's objection is based on line drawings of isolated petrosals published by Luo (1994). Needless to say, the orientation of the oval window is highly dependent on the position of the petrosal in the skull. In Kermack et al.'s (1981: figs. 90, 92) restoration of the skull of *Morganucodon*, the fenestra vestibuli approaches the vertical. The same condition is illustrated for *Morganucodon* and *Sinoconodon* by Crompton and Sun (1985: figs. 2, 4) and for *Megazostrodon* by Gow (1986: figs. 3, 4). Our survey of soricids, including *Scutisorex*, reveals a degree of ectotympanic inclination resembling that of 23° reported for *Cryptotis parva* by Henson (1961). This is approximated by the anter-

oventrolateral oval window of *Scutisorex* reported by Meng and Wyss (1996).

We have surveyed the ectotympanic and oval window inclination in other generalized living mammals in the Department of Mammalogy of the American Museum. Allin's proposal remains a useful approximation, but needs to be constrained. In all forms examined, the ectotympanic was more horizontally positioned than indicated by the plane of the fenestra vestibuli. The difference was not very striking, estimated as up to 20° in a few extreme cases (e.g., some *Talpidae*), but usually smaller than that. Additionally, in most marsupials, the anteroposterior plane of the tympanic membrane was not parallel to the anteroposterior plane of the fenestra vestibuli. The membrane converged medially from front to back; the reverse was true for the oval window. These observations show that the fenestra vestibuli can be used to approximate the orientation of the tympanic membrane. Moreover, the approximation seems to be valid for a wide range of forms, from *Morganucodon* to most living therians. Functionally, this correspondence seems related to the pistonlike movement of the stapes at the oval window (Høgmøen and Gundersen, 1977). In columnar stapes, the shaft is perpendicularly oriented with respect to the plane of the footplate, and in bicurrate stapes, the head is placed on, or close to, the axis lying perpendicular to the center of the footplate (Doran, 1878; Fleischer, 1973; Novacek and Wyss, 1986).

Using the method of Allin to estimate ectotympanic inclination, multituberculates exhibit both horizontal and inclined states. Isolated taeniolabidid petrosals from the Late Cretaceous attributed to *Catopsalis joyneri* resemble *Lambdopsalis*, with oval windows ventrally- and moderately anteriorly directed. In contrast, Late Cretaceous taeniolabidids, such as *Catopsbaatar* (Kielan-Jaworowska, 1974) and the more generalized *Kamptobaatar* (Kielan-Jaworowska, 1971, 1974), do not have ventrally directed oval windows, but ones that are ventrolateral and predict an inclined ectotympanic. The Late Cretaceous *Chulsanbaatar*, *Kryptobaatar*, and *Nemegtbaatar*, and the pilodontoids *Ptilodus* and *Ectypodus* also have oval windows that predict an inclined ectotympanic. The condition

in the Early Jurassic paulchoffatiids is currently unsettled; some specimens seem to have an almost ventral orientation of the oval window (Hahn, 1988), whereas others are at least inclined (Lillegraven and Hahn, 1991). These differences are probably a result of the extensive distortion to which these specimens were subjected during fossilization. Given the above distribution, the horizontal condition present in *Lambdopsalis* can hardly be considered the primitive one for multituberculates. In fact, the oval window inclination in the Late Cretaceous cimolodonts suggests a tilted tympanic membrane as primitive for those groups and for multituberculates as a whole, given that the condition in paulchoffatiids is uncertain. As an aside, it may be worthwhile to note that the multituberculates with a ventrally directed fenestra vestibuli are those with a greatly expanded vestibular apparatus (Miao, 1988; Luo and Ketten, 1991; Meng and Wyss, 1995). In light of such extreme specialization, the assumption of Meng and Wyss (1995) that *Lambdopsalis* is representative of Multituberculata as a whole with regard to auditory morphology seems problematic.

Our scoring for the inclination of the ectotympanic in Placentalia requires comment. A long-standing controversy concerning the primitive placental ectotympanic orientation exists in the literature. The original proposal of a near-horizontal ectotympanic as primitive for Placentalia by Kampen (1905) has been repeated by numerous subsequent authors, including us (Novacek, 1977, 1993; Rougier et al., 1996). In contrast, others (e.g., MacPhee, 1981; Rowe, 1988) have argued for a more inclined ectotympanic as the primitive placental condition. The ectotympanic is near-horizontal (up to 30°) in most lipotyphlans (Henson, 1961; MacPhee, 1981), but is more highly inclined in most other living placentals surveyed by us, including xenarthrans and pholidotans and is reported to be 45° in the Late Cretaceous *Asioryctes* and *Kennalestes* (Kielan-Jaworowska, 1981) and between 35 and 50° in early Tertiary *Leptictis* (Novacek, 1986). Consequently, when this feature is optimized under most of the recently advanced phylogenetic trees of ordinal interrelationships (e.g., Novacek, 1992a, b; Gaudin et al.,

1996), an inclined condition for the ectotympanic is likely primitive for Placentalia.

An additional character of the angular (ectotympanic) taken from Meng and Wyss (1995) is included in our phylogenetic analysis (appendix 1: 60). The angular is attached to the lower jaw, removed from the basicranium in non-mammalian cynodonts, but is detached from the jaw, positioned near the basicranium in mammals. Meng and Wyss (1995) treated the jaw and basicranial relationships of the angular as separate characters, but we have combined these here because when the angular is detached from the lower jaw, it invariably approaches the basicranium.

PHYLOGENETIC ANALYSIS

To test whether any features of the middle-ear ossicles represent synapomorphies of multituberculates and monotremes as suggested by Meng and Wyss (1995), the characters discussed above are evaluated in the broader context of basicranial anatomy across Mammaliaforma. The basis for this evaluation is the matrix of 20 taxa and 51 characters of the basicranium, exclusive of the auditory ossicles, developed by Rougier et al. (in press). Other matrices based on cranial and/or postcranial characters in mammaliaforms are available (e.g., Rowe, 1988; Wible, 1991; Luo, 1994), but the one in Rougier et al. (in press) is the most up-to-date taxonomically, including all mammaliaforms for which basicrania are known. Moreover, merging the ossicular data with that from the basicranium is justified, because these two anatomical regions are intimately linked. For the future, our goal is to expand this matrix and analysis by incorporating other cranial (including neural) and postcranial features as well as more taxa as they become known.

To the 51 basicranial characters (appendix 1: 1–51) from Rougier et al. (in press) and the eight ossicular characters already discussed (appendix: 52–60), two other features of the malleus are added (appendix 1: 61–62), both of which are taken from Meng and Wyss (1995). The first concerns whether or not the articular and prearticular are attached to the lower jaw. The second is the pres-

ence/absence of the manubrium mallei extending to the center of the tympanic membrane.

Meng and Wyss (1995) evaluated the distribution of 16 auditory characters across five mammaliaform taxa (i.e., *Morganucodon*, *Multituberculata*, *Monotremata*, *Marsupialia*, and *Placentalia*) plus an unspecified outgroup. Of their 16 characters, ten were from the ossicles, five were from the cochlea, and the remaining one concerned the external auditory meatus. Seven of their ten ossicular characters are included in our analysis (appendix 1: 55–57, 59–62). We have detailed above our reasons for excluding the character concerning the contact between the ectotympanic and “pterygoid” and for merging the two angular characters of jaw and basicranial relationships into one. The other ossicular character of Meng and Wyss (1995) excluded here concerns the size of the anterior process of the malleus, which is reported by these authors to be thinned and reduced in therians compared to the condition in the remaining taxa. Because Meng and Wyss (1995) do not specify a point of reference (e.g., anterior process is thinned and reduced compared to the length of the ectotympanic), we are unable to evaluate this character. Moreover, we note that the size of the anterior process relative to the ectotympanic of many generalized therians as well as that thought to be primitive for Theria is similar to that of monotremes (Fleischer, 1973). The five characters of the cochlea used by Meng and Wyss (1995) represent synapomorphies of Theria; three of these are included in the matrices of Wible et al. (1995), Rougier et al. (in press), and the current analysis (appendix 1: 6, 7, 11). Excluded are the radial pattern of the cochlear nerve and the basal extension of the basilar membrane; these are redundant on characters already included (appendix 1: 6, 7): a cochlea coiled more than 360° and a secondary osseous spiral lamina. Finally, the character of the external auditory meatus used by Meng and Wyss (1995: 143)—medial extension of the external auditory meatus to ventral side of the promontorium—represents a synapomorphy of Mammalia. We exclude it, because the medial position of the external auditory meatus is contingent on the location and inclination of the ecto-

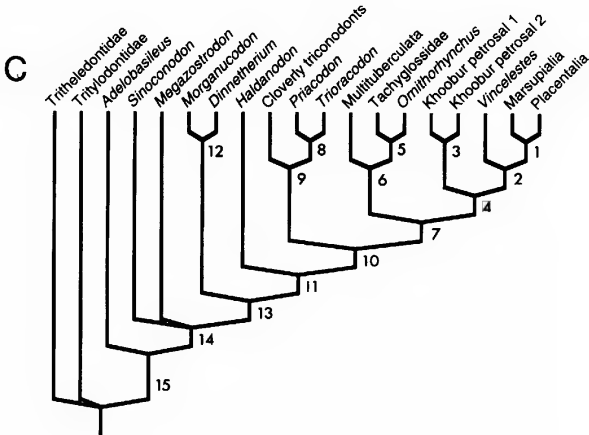
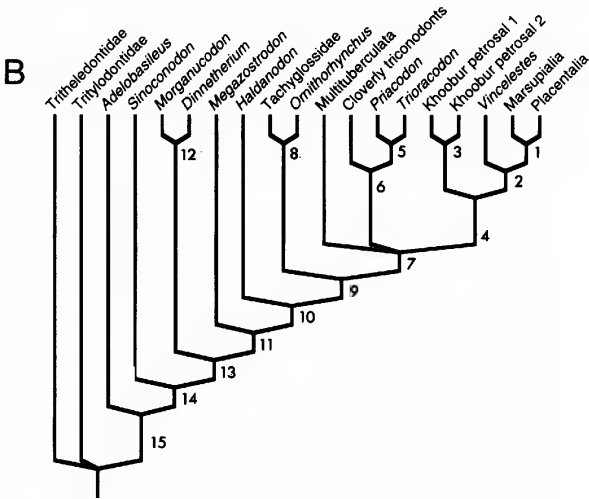
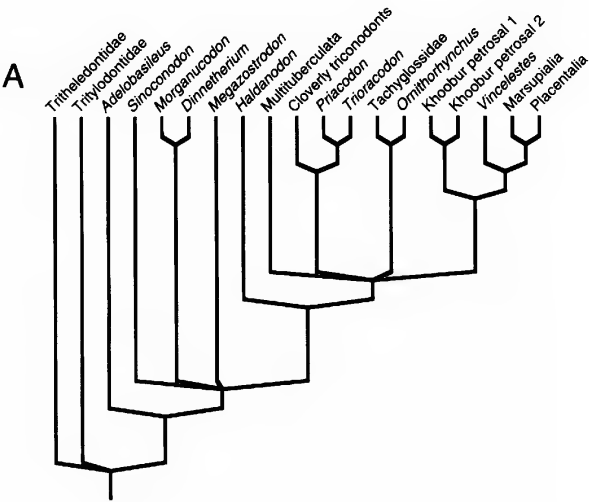
tympanic, which are already coded (appendix 1: 59, 60).

Along with adding eleven ossicular characters to the matrix of 51 basicranial characters from Rougier et al. (in press), our analysis differs in that we exclude one of their 18 ingroup taxa, the Late Jurassic triconodontid *Triconodon mordax*. In the strict consensus trees in Rougier et al. (in press), *Triconodon* fell at an unresolved trichotomy with the other two triconodontid taxa, *Trioracodon* and *Priacodon*. In the matrix combining basicranial and ossicular characters, *Triconodon* has the most missing entries, being 27.4% complete; the next most incomplete are the Cloverly triconodonts at 59.7% complete. Following a procedure for coping with abundant missing entries in Wilkinson (1995), *Triconodon* is removed from our analysis because it is a taxonomic equivalent of *Priacodon*; that is, it is not demonstrably different with respect to phylogenetically informative characters (p. 505). Removal of *Triconodon* has no effect on the tree position of the remaining taxa in the most parsimonious trees, but lowers the total number of trees.

A matrix of 62 characters across 19 taxa was compiled (appendix 2), including all the cranial characters supporting a multituberculate/monotreme clade published in previous cladistic analyses with the few exceptions already noted. The matrix was analyzed using the branch and bound algorithm of PAUP (Swofford, 1993). Multistate characters were not ordered; polymorphisms were treated as uncertainties. The outgroups and ingroups employed followed Rougier et al. (in press). Four equally most parsimonious trees were identified. The strict consensus of these (fig. 6A) is not as resolved as that produced by running the basicranial characters alone, with the major differences being the resolution of the Late Triassic–Early Jurassic mammaliaforms and the position of Monotremata. Whereas the relationships among *Adelobasileus*, *Sinoconodon*, Morganucodontidae, and *Megazostrodon* are fully resolved in the basicranial tree, these taxa with the exception of *Adelobasileus* are collapsed at a multichotomy in the combined tree. Similarly, monotremes are resolved out from the remaining three mammalian clades (multitu-

berculates, triconodonts, and prototribosphenidans + isolated petrosals from the Early Cretaceous of Mongolia) in the basicranial tree, but are collapsed at a multichotomy with these three clades in the tree obtained by combining the basicranial and ossicular characters.

Among the four most parsimonious trees, two different positions for multituberculates and monotremes are obtained. Two trees duplicate the results of the PAUP analysis of the basicranial characters alone: that is, monotremes are resolved out and the three other mammalian clades (multituberculates, triconodonts, and prototribosphenidans + isolated petrosals from Mongolia) fall at an unresolved trichotomy. Additionally, the relationships among the Late Triassic–Early Jurassic mammaliaforms are fully resolved. The strict consensus of these two trees is shown in figure 6B and diagnosed in appendix 3 (tree #1). In the remaining two trees, a multituberculate/monotreme clade is identified as the sister group of prototribosphenidans + isolated petrosals from Mongolia, and *Sinoconodon*, *Megazostrodon*, and Mammaliaformes are at a multichotomy. The strict consensus of these three trees is shown in figure 6C and is diagnosed in appendix 3 (tree #2). The multituberculate/monotreme clade is supported by two unequivocal and six equivocal synapomorphies (appendix 3: tree #1, node 6). The unequivocal characters are a flat incus and an anterior lamina contacting the orbitosphenoid. Whereas both of these occur in monotremes, their distributions in multituberculates are not well known: as detailed above, the flat incus is known only for *Chulsanbaatar* and *Lambdopsalis*, and the expanded anterior lamina is known only for Late Cretaceous specimens from Mongolia (Wible and Hopson, 1993). Among the equivocal characters are two from the ossicles: a columnar stapes and an incus lying dorsal to the malleus. Again, as detailed above, both of these occur in monotremes, but a columnar stapes is known only for *Lambdopsalis*, with stapes of other shapes inferred to be present in other multituberculates, and an incus dorsal to the malleus is not known for any multituberculate. In the consensus tree in which monotremes are the outgroup to multituberculates and other



mammals (fig. 6A), a flat incus lying dorsal to the malleus and a columnar stapes are unequivocal synapomorphies of Monotremata (appendix 3: tree #1, node 8).

As is apparent from the unresolved relationships within Mammalia in the strict consensus of the four most parsimonious trees (fig. 6A), combining the ossicular data with that from the basicranium does not resolve whether or not any ossicular characters are synapomorphies of a multituberculate/monotreme clade. The two most extensive cranial data sets published to date, which are not as taxonomically inclusive as the analysis here, yield conflicting results with regard to multituberculates and monotremes; in Rowe (1988), multituberculates are closer to therians than are monotremes, whereas this is reversed in Wible (1991). However, these relationships are not strongly supported in either analysis. Fewer postcranial data sets have been published, but yield more consistent results; in both Rowe (1988) and Sereno and McKenna (1995), there is strong support for multituberculates being closer to therians than are monotremes (but see Kielan-Jaworowska and Gambaryan, 1994, for an opposing view). Correcting and combining these various data sets is beyond the scope of the current report. However, given the weight of the postcranial evidence in Rowe (1988) and Sereno and McKenna (1995), it seems likely that closer affinities with therians will be supported for multituberculates than for monotremes by the combined data set. As noted by Rougier et al. (1996), a matrix merging the ossicular data from Meng and Wyss (1995) with the postcranial data from Sereno and McKenna (1995) yields one phylogenetic tree that mirrors the results of the latter authors: that is, therian affinities for multituberculates. If this indeed is the out-

come when the various cranial and postcranial data sets are combined, then any resemblances in the ossicles of monotremes and multituberculates are convergent acquisitions.

Affinities of multituberculates and monotremes have been supported elsewhere based on other features. Broom (1914), for example, looked at the distribution of various cranial and postcranial characters among cynodonts, multituberculates, monotremes, marsupials, and placentals. He noted that multituberculates shared the most features with monotremes and proposed a close relationship for these two groups. Subsequent studies (e.g., Rowe, 1988) have shown that the features cited by Broom are plesiomorphies, such as an enlarged and elongated coracoid and an uncoiled cochlea. Moreover, it was revealed in a postscript added to Broom's article by W. Granger that the multituberculate coracoid discussed by Broom was incorrectly identified; this element is, in fact, part of the pelvis based on comparisons with newly recovered material. Kermack and Kielan-Jaworowska (1971: 103; see also Kielan-Jaworowska, 1971) also supported a close relationship between multituberculates and monotremes based on four features: (1) greatly reduced alisphenoid, (2) jugal absent, (3) lacrimal usually reduced or absent, (4) multituberculate ectopterygoid resembling the monotreme *Echidna* pterygoid. Of these four, only the reduced alisphenoid remains a valid resemblance of monotremes and multituberculates, the sole exception being the derived taeniolabidid *Lambdopsalis*, which has an enlarged alisphenoid (Miao, 1988). A jugal is present in *Ornithorhynchus* (Zeller, 1989) and has been described in various multituberculates (Hopson et al., 1989). A large lacrimal occurs in Late Jurassic paulchoffa-

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Fig. 6. **A**, Strict consensus of four most parsimonious trees resulting from PAUP analysis of matrix in appendix 2. Tree length = 169 steps; consistency index = 0.574; retention index = 0.706; these values in the four individual trees are 163, 0.595, and 0.731, respectively. **B**, Strict consensus of the two most parsimonious trees that supported monotremes as the outgroup to other mammals. This tree is diagnosed as Tree #1 in appendix 3, and the numbers here correspond to the diagnosed nodes. **C**, Strict consensus of the two most parsimonious trees that supported a monotreme/multituberculate clade. This tree is diagnosed as Tree #2 in appendix 3, and the numbers here correspond to the diagnosed nodes.

tiids (Hahn, 1969, 1987) and in Mongolian Late Cretaceous taxa (Kielan-Jaworowska et al., 1986; Hurum, 1994). Finally, a separate ectopterygoid is likely lacking in multituberculates (Miao, 1988).

In support of multituberculate/monotreme affinities, Meng and Wyss (1995) cited two recent studies: Hopson and Rougier (1993) and Wible and Hopson (1993). Of these two, only the latter truly supports a multituberculate/monotreme clade. Hopson and Rougier (1993) merely noted the presence of a derived feature in braincase structure in multituberculates and monotremes (an enlarged anterior lamina and reduced alisphenoid), which is already included in the current matrix. On the other hand, Wible and Hopson (1993) compiled a matrix of 38 basicranial characters across eleven ingroup taxa that identified a multituberculate/monotreme clade supported by one unequivocal synapomorphy (a common tympanic aperture for the prootic canal and pterygoparoccipital foramen) and five equivocal synapomorphies. The matrix in Wible and Hopson (1993) represents an early iteration in our ongoing studies of basicranial anatomy. As discussed above, subsequent matrices of basicranial characters in Wible et al. (1995) and Rougier et al. (in press) include the relevant characters from Wible and Hopson (1993) and yield different results, identifying monotremes as the outgroup to multituberculates and other mammals. These matrices differ in several regards from that in Wible and Hopson (1993). In addition to refining character identification and correcting missing data based on newly published specimens, the matrices in Wible et al. (1995) and Rougier et al. (in press) expand both the number of characters (to 44 and 51, respectively) and the number of ingroup taxa (to 15 and 18, respectively). Moreover, the matrix in Rougier et al. (in press) treats *Ornithorhynchus* and *Tachyglossidae* as separate OTUs. These taxa differ in numerous regards: for example, a common tympanic aperture for the prootic canal and pterygoparoccipital foramen is present in the platypus, but not in the echidnas (Wible and Hopson, 1993, 1995). In prior cladistic analyses (e.g., Rowe, 1988; Wible and Hopson, 1993; Wible et al., 1995), monotremes were scored by reconstructing an ancestral

state in instances where more than one condition was present. This approach relied on a preconceived notion about the direction of evolutionary transformation in monotremes, failing to test the monophyly of the group, and introduced a potential source of error: attribution of false ancestral states.

ORIGIN OF MIDDLE-EAR OSSICLES

The remarkable uniformity in the structure and morphology of the mammalian middle-ear ossicles has been emphasized repeatedly (e.g., Kemp, 1983; Miao and Lillegraven, 1986; Novacek, 1993; Meng and Wyss, 1995; Presley, 1995; this report). Nevertheless, whether these elements were detached from the lower jaw a single (e.g., Patterson, 1981; Rowe, 1995) or multiple times (e.g., Simpson, 1961; Allin and Hopson, 1992) has been and remains a controversial issue. Several decades ago, when a polyphyletic origin of Mammalia was the dominant view (e.g., Olson, 1944; Patterson, 1956; Simpson, 1961), a recurrent argument was that the structure of the postdentary bones preadapted them to become ear ossicles and, therefore, the repetitive detachment of these elements from the lower jaw was to be expected. With multiple origins of mammals, those taxa with a single lower jaw bone and a complex middle-ear ossicular chain constituted a grade, not a clade (Kirsch, 1984). However, independent detachment of the ossicles from the jaw cannot be justified without a cladistic framework (see comments in Novacek, 1993).

Later, the dominant view was that of a basal dichotomy in the origin of mammals, with monophyly supported by some (e.g., Hopson and Crompton, 1969; Hopson, 1970; Jenkins and Crompton, 1979) and diphyley by others (e.g., Kermack, 1967). The two groupings were Prototheria or Atheria for monotremes, multituberculates, docodonts, and triconodonts; and Theria for marsupials, placentals, and extinct relatives. Supporting this dichotomy were two characters, one concerning the pattern of molar cusps and the other the composition of the side wall of the braincase. Given that the basal members of both Prototheria and Theria had postdentary bones attached to the lower jaw, at least two inde-

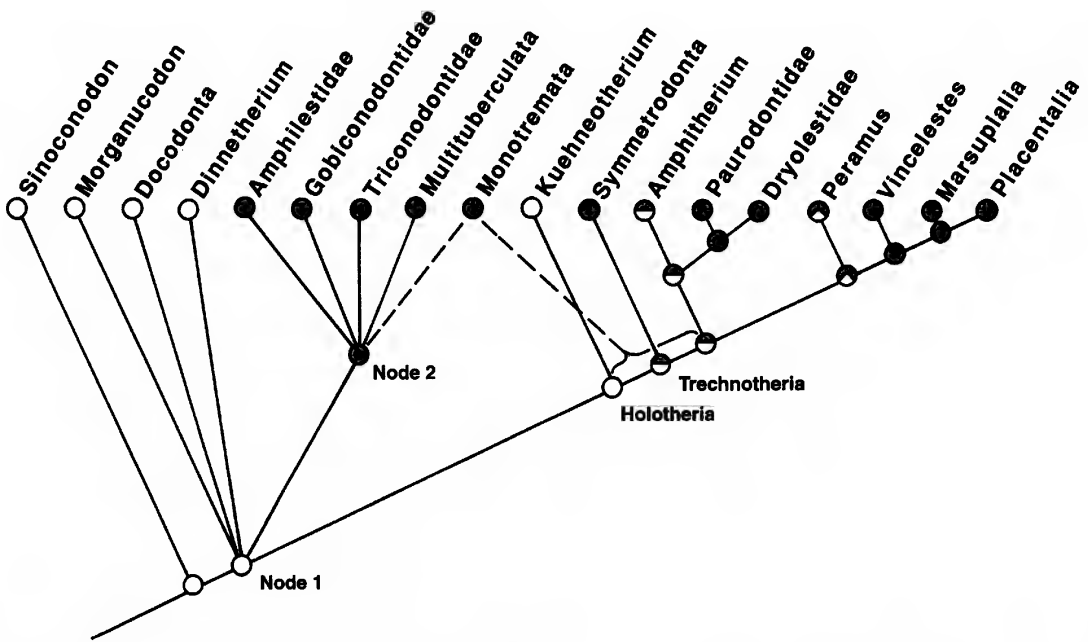


Fig. 7. Allin and Hopson's (1992: fig. 28.13) cladogram showing their preferred hypothesis of mammaliaform interrelationships. Open circles represent the primitive condition of postdentary bones attached to the lower jaw; partial black circles represent partial attachment; and completely black circles represent ear ossicles fully separated from lower jaw. Reprinted with authors' permission.

pendent origins of suspended ossicles were required, in monotremes and multituberculates on the one hand and in marsupials and placentals on the other. The two supposed synapomorphies of prototherians have been held by later researchers to be either plesiomorphies (Kemp, 1983) or present in the derived condition in only some purported members (Hopson and Rougier, 1993).

The morphological basis for the monophyly of Prototheria was undermined by observations on the development of the side wall of the braincase in living mammals (Griffiths, 1978; Presley, 1981). Integration of the neontological and paleontological evidence by Patterson (1981) and Kemp (1983) resulted in cladograms dispersing the members of Prototheria into a paraphyletic series and explicitly supporting the single origin of definitive middle-ear ossicles. All subsequent cladistic analyses (e.g., Rowe, 1988, 1983; Wible, 1991; Lillegraven and Krusat, 1991; Crompton and Luo, 1993; Rougier et al., 1996) have confirmed the paraphyletic nature of Prototheria. Consequently, the independent origin of ear ossicles in monotremes and

therians can no longer be defended based on a basal mammalian (mammaliaform) dichotomy. Although the majority of authors currently support the monophyly of Mammalia, several (i.e., Lillegraven and Krusat, 1991; Miao, 1991; Kielan-Jaworowska, 1992; Kielan-Jaworowska and Gambaryan, 1994) still consider polyphyly as a viable alternative.

Recently, Allin and Hopson (1992) have argued for the multiple origin of ear ossicles in mammals, based on incongruity between the phylogenetic results obtained considering dental features on the one hand and lower jaw morphology (postdentary bones) on the other. As support for their interpretation, Allin and Hopson (1992) presented a phylogeny of mammaliaforms (reproduced here as fig. 7). They followed Prothero (1981) on relationships within Trechnotheria (McKenna, 1975), but the arrangement of taxa basal to Holotheria (Hopson, 1994) is presented without rationale or reference to any source. The sister group to Holotheria is indeterminate because a multichotomy including most of the Jurassic mammaliaforms is the next node (fig. 7: node 1). Included at this multichoto-

my is an unusual monophyletic assemblage consisting of Amphilestidae, Gobiconodontidae, Triconodontidae, Multituberculata, and possibly Monotremata (fig. 7: node 2). Cladistic analyses do not support node 2 and frequently show a paraphyletic series for some of these taxa (Rowe, 1988, 1993; Wible, 1991; Wible et al., 1995; Rougier et al., 1996). If Allin and Hopson's tree is correct, it implies the independent acquisition of definitive ear ossicles a minimum of two times, at node 2 and at Trechnotheria, or a single origin at node 1 with a minimum of one reversal in *Kuehneotherium*. However, we reiterate that no characters supporting their tree are provided and, therefore, we are unable to further evaluate their hypothesis. Two additional issues of Allin and Hopson's (1992) proposal—the position of *Kuehneotherium* and the transformations of the postdentary elements within Holotheria—are treated below.

(1) Relationships of *Kuehneotherium* and Its Allies

Kuehneotherium praecursoris from the Early Jurassic of England known only from lower jaws and isolated dental material (Kermack et al., 1968) presents conflicting sets of characters. On the one hand, the lower jaw of *Kuehneotherium* has a deep trough and medial ridge, which when compared with basal mammaliaforms, such as *Morganucodon*, suggests that the postdentary bones retained the primitive attachment to the dentary (Kermack et al., 1968). On the other, the molars of *Kuehneotherium* share with therians a triangular arrangement of cusps, which has been used (e.g., Crompton and Jenkins, 1979; Prothero, 1981) to ally *Kuehneotherium* closer to therians than are monotremes and multituberculates, which already have suspended ossicles. As discussed below, this dental character cannot be used to exclude either multituberculates or monotremes from being more closely related to therians than is *Kuehneotherium*.

Multituberculates have such a derived dentition that no hypothesis of homology between their molar cusps and those of other mammaliaforms can be established. In fact, use of the terms molar and premolar in the multituberculate dentition does not imply

strict homology with those teeth in therians (Simmons, 1988). According to Kemp (1983), multituberculate origins are equally likely from holotherian or prototherian dental patterns.

Recently recovered dental remains of extinct monotremes (Archer et al., 1985, 1992, 1993; Flannery et al., 1995) have been used to advance trechnotherian relationships for Monotremata. Yet, the phylogenetic information yielded by the monotreme dentition is equivocal as illustrated by the various positions that monotremes have been assigned within Trechnotheria. Affinities have been proposed with tribosphenidans (Archer et al., 1985), advanced peramurids (Kielan-Jaworowska et al., 1987), dryolestoids (Bonaparte, 1990; Archer et al., 1993), and symmetrodonts (Hopson, 1994). However, not all authors (e.g., Archer et al., 1992; Wible et al., 1995) accept trechnotherian affinities for monotremes. Flannery et al. (1995: 419) stated that the basic monotreme molar structure is not therian-like [holotherian], and that any other similarities between monotremes and therians [holotherians] may be convergent. These doubts about the similarities shared by monotreme and therian dentitions are congruent with other phylogenetic studies based on different character systems, which place multituberculates and/or triconodonts between monotremes and the early members of the therian lineage (Rowe, 1988, 1993; Wible et al., 1995; Rougier et al., in press). If these tree topologies are accepted, close relationships of monotremes and any clade of trechnotherians are insupportable.

Only two of the 62 characters considered in this study (appendix 1) can be scored for *Kuehneotherium*—the attachment of the angular and of the prearticular/articular to the lower jaw (60, 61). For both, *Kuehneotherium* presents the plesiomorphic condition. Consequently, *Kuehneotherium* is a taxonomic equivalent (Wilkinson, 1995) of all outgroups to Mammalia, and its phylogenetic position can be anywhere between that clade and the root of the tree. Given our uncertainties about the trechnotherian affinities of monotremes and the absence of trechnotherian synapomorphies in the dentitions of multituberculates and triconodonts, it is unlikely that the triangular arrangement of molar

cusps occurring in *Kuehneotherium* and therians is homologous.

In addition to *Kuehneotherium*, trechnotherians, and monotremes, there are other taxa that show, to differing degrees, a triangular pattern to their molar cusps: some docodonts (Kermack et al., 1987), *Tegotherium* (Tatarinov, 1994, but see Hopson, 1995), and *Shuotherium* (Chow and Rich, 1982). We are unaware of any phylogenetic proposal that would consider the origin of a triangular molar pattern a single event in mammaliaform evolution and, thus, this morphology was acquired convergently at least among some of these taxa. Furthermore, similarities in the occlusal pattern of *Kuehneotherium*, *Megazostrodon*, and amphilestids have been repeatedly stressed (e.g., Mills, 1971; Crompton, 1974; Crompton and Jenkins, 1979). The supposedly derived pattern shared by these taxa may suggest in fact that the therian molar pattern of *Kuehneotherium* could be plesiomorphous for a more inclusive group. Crompton (1974: 429) recognized two features discriminating *Kuehneotherium* and *Megazostrodon*: 1) the way in which the adjoining lower molars meet one another and 2) the rotation of some subsidiary cusps to form shearing planes oriented obliquely to the longitudinal axis of the jaw. The condition occurring in *Kuehneotherium* with regard to both features is present in other taxa: the first, in amphilestids and docodonts, and the second, as stated above, in monotremes, some docodonts, and several other taxa of uncertain affinities, such as *Shuotherium*. In diagnosing Holotheria (his Theria), Prothero (1981) used the molar features of Crompton (1974), adding to them the absence of a Kühnecone (cusp g). This cusp, however, is also absent in triconodonts, including amphilestids, and presumably in multituberculates. Additionally, in conflict with Prothero's diagnosis, the *Kuehneotherium*-like taxon *Woutersia* has a well-developed Kühnecone (Sigogneau-Russell and Hahn, 1995). Prothero (1981) also considered the oblique arrangement of the occlusal facets and the presence of a single broad wear facet on the anterior trigon/posterior trigonid as a holotherian synapomorphy. With wear on their molars, amphilestids also have a single broad wear facet between the principal cusp and the

anterior one in the upper molars and between the principal cusp and the posterior one in the lowers, much as in *Kuehneotherium* (Mills, 1984). The facets in amphilestids are largely aligned anteroposteriorly instead of obliquely as in holotherians, but this orientation is linked to the disposition of the cusps. The phylogenetic importance of these facets is uncertain, because as Mills (1984) shows, the wear facets of kuehneotheriids and amphilestids both develop from apical facets that unite with wear. From the above comments, it is apparent that our current understanding of the dental transformations in basal mammaliaforms is far from complete and that the evidence linking *Kuehneotherium* with trechnotherians is inconclusive.

Including two other taxa thought to be closely related to *Kuehneotherium*, i.e., *Woutersia* (Sigogneau-Russell, 1983; Sigogneau-Russell and Hahn, 1995) and *Shuotherium* (Chow and Rich, 1982), in recent cladistic hypotheses also poses problems. *Woutersia* is known only from isolated teeth and, though originally included in Kuehneotheriidae (Sigogneau-Russell, 1983) has recently been assigned to a family of its own, Woutersiidae, within Holotheria (Sigogneau-Russell and Hahn, 1995). Yet, the latter authors also observed that *Woutersia* shares some derived characters with upper molars of docodonts (p. 245). Sigogneau-Russell and Hahn (1995) ultimately excluded docodont affinities for *Woutersia*, but the observed similarities emphasize that alternative interpretations of the tooth morphology of kuehneotheriids are feasible. *Shuotherium*, known from a single lower jaw, shows evidence for the retention of postdentary bones (Chow and Rich, 1982). When coded for the characters in our matrix, *Shuotherium* is a taxonomic equivalent of *Kuehneotherium* and occupies a similar array of positions in our tree. Consequently, the previous comments regarding the conflicting characters of dental and lower jaw morphology made for *Kuehneotherium*, also apply for *Shuotherium*.

(2) Transformations of the Postdentary Elements Within Holotheria

Allin and Hopson (1992) proposed that symmetrodonts, dryolestids, and prototribosphenidans independently acquired the defin-

itive triossicular middle ear (fig. 7). This conclusion resulted from their restoration of postdentary bones not completely freed from the lower jaw in two taxa nested within Trechnotheria, namely *Amphitherium* and *Peramus* (fig. 7). In support of their restoration, Allin and Hopson (1992) noted shallow scars in the vicinity of the mandibular foramen in both taxa (more developed in *Amphitherium*). Their illustration of *Amphitherium* (Allin and Hopson, 1982: fig. 28.11) shows facets supposedly for the prearticular and angular as well as the coronoid and splenial. The postdentary elements are not preserved in either taxa, and it is, therefore, difficult to corroborate their reconstruction. However, alternative interpretations of these scars in the lower jaw are possible. The facet for the supposed angular is continuous with that for the splenial, and the latter bone may account for both facets. A similar restoration for the splenial within divided facets has been reported previously for dryolestids (Krebs, 1971; Martin, 1995). The facet for the supposed prearticular is continuous with the Meckelian groove and, in fact, may be a facet for a persisting Meckelian cartilage, which is retained into postnatal life among monotremes (Kuhn, 1971; Zeller, 1989) and marsupials (Maier, 1987; Filan, 1991).

Without specimens showing the actual relationships of the postdentary elements, restorations such as that of Allin and Hopson (1992) are possible, but not substantiated. Alternative interpretations for the scars in *Amphitherium* and *Peramus* preclude a serious challenge to the well-supported monophyletic origin of the ear bones. The reported evidence is limited and ambiguous. As Allin and Hopson (1992) remarked, whatever the ultimate solution to the problem, it is unlikely that the dental and craniomandibular morphology can be reconciled in a single cladogram; one or the other, or both, will include purported synapomorphies that are in fact homoplasies.

CONCLUSIONS

The fossil evidence presented here joins contributions on multituberculate ear ossicles published in the past decade (Miao and Lillegraven, 1986; Miao, 1988; Meng, 1992;

Meng and Wyss, 1995, 1996; Hurum et al., 1995; Rougier et al., 1996), which have spurred intensive research on the auditory region of mammaliaforms. Recent cladistic studies (Wible and Hopson, 1993; Meng and Wyss, 1995) have revived older proposals (e.g., Broom, 1914) that multituberculates are the sister group of monotremes. After critical review of the auditory structures advanced in support of this clade, ossicular characters are evaluated in the more general framework of basicranial evolution across Mammaliaforma. It is shown here that the ossicular and basicranial characters yield inconclusive results concerning the relative positions of multituberculates and monotremes with regard to other mammaliaforms. However, under any of the possible solutions, multituberculates are mammals. The addition of other character systems, such as the postcranium (Rowe, 1988; Sereno and McKenna, 1995), to the analysis seems to support a closer relationship of multituberculates with therians than with monotremes. In spite of these contributions, a coherent picture of the primitive multituberculate ear morphology is hindered by the scanty evidence provided by the incomplete specimens now available. Without new material, opposing interpretations of the fragmentary material cannot be settled.

Whether or not the middle-ear ossicles were detached from the lower jaw a single or multiple times during mammaliaform evolution is an enduring controversy. From comparisons of the middle-ear ossicles of multituberculates with those of living mammals, we find no basis to doubt a priori the homology of any of the elements of multituberculates, monotremes, and therians. Furthermore, the results of our cladistic analysis are fully congruent with a single origin of the definitive middle-ear ossicles and therefore suggest convergent acquisition of a triangular molar pattern in *Kuehneotherium* and trechnotherians.

Our hypothesis is effected by the ultimate resolution of the phylogenetic relationships of some very incomplete taxa, such as *Kuehneotherium*, *Shuotherium*, and *Woutersia*. The dental homologies among these taxa and morganucodontids, docodonts, multituberculates, monotremes, and trechnotherians are

controversial, though several hypotheses have been proposed (e.g., Patterson, 1956; Crompton, 1971, 1974; Prothero, 1981). Given the large number of taxa diagnosed primarily from dental remains, a unified view of postcanine evolution among Mammaliaformes is essential in order to integrate dental evidence into the data sets of cranial and postcranial character complexes, which allow comprehensive hypotheses of homology encompassing a wide array of taxa.

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APPENDIX 1

BASICRANIAL AND OSSICULAR CHARACTERS

1. Petrosal promontorium—absent (0) or present (1).
2. Para/basisphenoid wing—present (0) or absent (1).
3. Cochlear housing shape—indistinct (0), triangular in outline, wider posteriorly with steep lateral wall (1), triangular in outline, wider posteriorly without steep lateral wall (2), or fingerlike in outline (3).
4. Ventral crest on cochlear housing—absent (0) or present (1).
5. Small foramen on cochlear housing anteromedial to fenestra vestibuli—absent (0) or present (1).
6. Cochlear duct—short (0), elongate and straight (1), bent (2), or coiled, 360° or more (3).
7. Secondary spiral lamina—absent (0) or present (1).
8. Semicircular canals enclosed by petrosal only—absent (0) or present (1).
9. Fenestra vestibuli shape—rounded, stapedial ratio less than 1.2 (0) or ellipsoidal, stapedial ratio greater than 1.4 (1).
10. Fenestra vestibuli margin—with thickened osseous ring (0) or without osseous ring (1).
11. Channel for perilymphatic duct—no indication (0), open sulcus (1), partially enclosed by bony lappets (2), or fully enclosed to form a canal, a cochlear aqueduct (3).
12. Lateral opening of cochlear aqueduct—absent (0), medial (external) to perilymphatic foramen (1), or within inner ear (2).
13. Jugular fossa including jugular foramen and perilymphatic foramen/fenestra cochleae—present (0) or absent (1).
14. Jugular foramen size relative to perilymphatic foramen/fenestra cochleae—equal to or larger (0) or smaller (1).
15. Crista interfenestralis—tall and horizontal, extending to base of paroccipital process (0), vertical, delimiting back of promontorium (1), or not distinguishable from surrounding elements (2).
16. Fossa for stapedius muscle—absent (0), on crista interfenestralis (1), or lateral to crista interfenestralis (2).
17. Paroccipital process—not extending ventral to level of cochlear housing (0) or extending ventral to level of cochlear housing (1).
18. Caudal tympanic process of petrosal—absent (0) or present (1).
19. Post-promontorial tympanic recess—absent (0) or present (1).
20. Deep pocket medial to paroccipital process—absent (0) or present (1).
21. Tympanohyal—separate (0), attached to petrosal, posteromedially directed (1), or attached to petrosal, medially directed (2).
22. Tympanohyal/promontorial contact—absent (0) or present (1).
23. Crista parotica/squamosal contact—present (0) or absent (1).
24. Fossa incudis or quadrate articulation on petrosal—absent (0) or present (1).
25. Epitympanic recess on petrosal—absent (0) or present (1).
26. Cranial aperture of prootic canal—absent (0), in rear of cavum epiptericum (1), between the cavum and anterodorsal margin of subarcuate fossa (2), or at anterodorsal margin of subarcuate fossa (3).
27. Tympanic aperture of prootic canal—absent (0), separate from (1), or confluent with pterygoparoccipital foramen (2).
28. Pterygoparoccipital foramen—at same level or posterior to fenestra vestibuli (0), anterior to it (1), or absent (2).
29. Lateral flange—laterally directed shelf (0), with vertical and horizontal components in lateral view (1), ventrally directed crest (2), contacting cochlear housing (3), or greatly reduced in size (4).
30. Lateral flange/crista parotica relationship—narrowly separated (0), widely separated (1), continuous (2), or lateral flange greatly reduced (3).
31. Vascular foramen in lateral flange—absent (0) or present (1).
32. Post-trigeminal canal—absent (0) or present (1).
33. Facial ganglion floor—open ventrally (0), broad petrosal bridge, flooring part of hyomandibular and palatine rami (1), or narrow petrosal bridge, flooring only primary facial foramen (2).

34. Lateral trough of petrosal—absent (0) or present (1).
35. Cavum epiptericum floor—open ventrally (0), partially floored by petrosal (1), floored, primarily by petrosal (2), or floored, primarily by alisphenoid (3).
36. Tensor tympani fossa—indistinct (0), deep recess on lateral trough anterior to hiatus Fallopii (1), or deep recess on lateral trough posterior to secondary facial foramen (2).
37. Petrosal contact with quadrate ramus of alisphenoid (epipterygoid)—elongate (0) or small or absent (1).
38. Internal acoustic meatus—without distinct medial rim (0) or with medial rim (1).
39. Pila antotica—ossified base present (0) or absent (1).
40. Wall separating cavum supracochleare from cavum epiptericum—absent (0), present with small fenestra (fenestra semilunaris) (1), or complete (2).
41. Sulcus for sigmoid sinus extending to jugular foramen—absent (0) or present (1).
42. Sulcus for inferior petrosal sinus—enclosed in petrosal, laterally directed at rostral end (0), between petrosal and basioccipital, anteroposteriorly directed (1), or endocranial (2).
43. Craniomandibular joint position relative to fenestra vestibuli—level with (0) or anterior to (1).
44. Thick, laterally directed surface of petrosal related to glenoid fossa—absent (0) or present (1).
45. Anterior lamina—separated externally from orbitosphenoid by alisphenoid (0), contacts orbitosphenoid (1), or absent (2).
46. Small vascular foramen in anterior lamina—absent (0) or present (1).
47. Number of trigeminal nerve exits posterior to alisphenoid—single (0), multiple (1), or none (2).
48. Ventral ascending groove or canal—open laterally (0), intramural, within petrosal (1), intramural, between petrosal and squamosal (2), endocranial (3), or absent (4).
49. Orientation of ventral ascending groove or canal—vertical (0), horizontal (1), or without groove or canal (2).
50. Dorsal ascending groove or canal—open laterally dorsal to posttemporal canal (0), intramural, covered laterally by parietal and/or squamosal (1), or endocranial (2).
51. Hypoglossal foramina—double or multiple (0), single (1), or confluent with jugular foramen (2).
52. Stapedial head—absent (0) or present (1).
53. Shaft of stapes—bicurrate, rectangular, crura equidistant from footplate margin (0), bicurrate, rectangular, crura anteriorly displaced (1), bicurrate, triangular (2), or single (3).
54. Stapedial foramen—well developed (0), microperforate (1), or absent (2).
55. Shape of quadrate (incus)—complex (0) or flat (1).
56. Relative position of quadrate (incus) to articular (malleus)—dorsal (0) or posterior (1).
57. Basicranial articulation of quadrate (incus)—broad (0) or limited to fossa incudis (1).
58. Shape of quadrate (incus) articulation with articular (malleus)—strongly convex (0) or weakly convex (1).
59. Orientation of angular (ectotympanic)—vertical or inclined (0) or horizontal (1).
60. Angular (ectotympanic)—attached to lower jaw, removed from basicranium (0) or detached, close to basicranium (1).
61. Prearticular and articular—attached to lower jaw (0) or detached (1).
62. Manubrium mallei extending to center of tympanic membrane—absent (0) or present (1).

APPENDIX 2

TAXON-CHARACTER MATRIX

Taxon	Character*													%compl.
	5	10	15	20	25	30	35	40	45	50	55	60		
Tritheledontidae	000N0	0?000	00000	00000	00000	00000	00000	00000	0?000	00000	00000	00000	00	96.8
Tritylodontidae	000N0	0?000	00000	10000	10110	00010	10A00	00102	0?000	01001	0?000	00000	00	95.2
Adelobasileus	10100	A??01	00000	00000	00?00	?1010	10011	0??0?	??000	01001	1????	?????	??	66.1
Sinoconodon	11110	00101	A0000	10000	00000	11010	10?11	00100	??000	01000	1?10?	???00	0?	83.9
Morganucodon	1110A	10101	10000	10000	00110	31010	10111	10000	10000	11001	1?100	00000	0?	96.8
Dinnetherium	11100	1?111	??000	1?000	00110	E1010	10D11	10???	???0A	?A00?	0????	???00	0?	61.3
Megazostrodon	11110	1?101	A00?0	10000	?0???	E1010	1?D11	?0?0?	??000	0000?	1???0	00000	0?	67.7
Haldanodon	11110	1?101	10110	11000	10110	21110	?0D12	00010	10000	1000D	1?100	0?000	0?	88.7
Multituberculata	11300	10111	D0A00	21A00	10011	32132	11212	21100	10001	01111	01?A1	?1101	1?	95.2
Clov. triconodonts	11300	1?111	??100	21000	10010	F1121	?0212	1???	??10A	?AB1?	1????	???0?	??	59.7
Priacodon	1130A	10111	20110	21001	D011?	21121	0?012	1?0?2	00?0A	1A211	1????	???01	1?	69.3
Trioracodon	11301	1?111	D0110	21001	10110	11121	00212	110?2	00?0A	1A211	?????	???01	1?	75.8
Khoobur petrosal 1	11300	10111	32101	21111	20000	21120	00212	111?1	0011?	??211	?????	???0?	??	75.8
Khoobur petrosal 2	11300	10111	31101	21?1?	?00??	21120	0?212	1?1?1	00?0A	0A211	?????	???0?	??	64.5
Vincelestes	11200	21111	32101	21110	20111	31122	A0112	01111	?0110	01111	0?C0?	???01	1?	88.7
Tachyglossidae	010N0	20101	31102	00000	11110	31143	01112	01102	02101	00201	21321	11111	11	100
Ornithorhynchus	11300	20101	10100	01000	21110	32122	00112	01100	02001	00000	21321	11111	11	100
Marsupialia	11200	31111	32101	21110	20A11	31243	00D03	01112	01102	02422	01FA0	01101	11	100
Placentalia	11200	31111	32101	21110	20A11	00143	00103	01112	0D102	02302	A1200	01101	11	100

*? = missing data; N = not applicable; 0-4 = character states (see appendix 1); A = 0 & 1; B = 0 & 2; C = 0 & 1 & 2; D = 1 & 2; E = 2 & 3; F = 1 & 2 & 3; % compl. = % of scoreable characters.

APPENDIX 3

DIAGNOSES OF NODES

Two trees are diagnosed here. As detailed in the text, PAUP analysis of the matrix in appendix 2 identified five equally most parsimonious trees. The first tree diagnosed is the strict consensus tree (fig. 6B) of the two most parsimonious ones in which monotremes are the outgroup to other mammals. The second tree is the strict consensus tree (fig. 6C) of the two most parsimonious ones in which a monotreme/multituberculata clade is supported. Nodes are diagnosed by listing the derived condition for characters in appendix 1. Multistate characters or reversals are depicted within parentheses following the character number. Asterisks (*) denote equivocal characters. Characters are optimized under an accelerated transformation (ACCTRAN) assumption.

Tree #1

Node 1. Theria

- 29 (4), 30 (3)—lateral flange greatly reduced
- 34(0)—lateral trough absent
- 35(3)—cavum epiptericum floored primarily by alisphenoid
- 40(2)—complete wall separating cavum supra-cochleare from cavum epiptericum
- 42(1)—sulcus for inferior petrosal sinus between

petrosal and basioccipital, anteroposteriorly directed

47(2)—no foramina for trigeminal nerve posterior to alisphenoid

50(2)—dorsal ascending groove endocranial

6(3)*—cochlear duct coiled

45(2)*—anterior lamina absent

48(3)*—ventral ascending groove endocranial

49(0)*—ventral ascending groove vertical

Node 2. Prototribosphenida

3(2)—cochlear housing triangular, wider posteriorly without steep lateral wall

7—secondary osseous spiral lamina

25—epitympanic recess on petrosal

33(1)—broad petrosal bridge flooring facial nerve branches

6(2)*—cochlear duct bent

23*—crista parotica/squamosal contact absent

36(0)*—tensor tympani fossa indistinct

48(1)*—ventral ascending canal intramural within petrosal

Node 3

26(2)—cranial aperture of prootic canal between cavum epiptericum and anterodorsal margin of subarcuate fossa

30(0)—lateral flange narrowly separated from crista parotica

20*—deep pocket medial to paroccipital process

24(0)*—fossa incudis on petrosal absent

Node 4

- 11(3)—cochlear aqueduct
- 12(2)—lateral opening of cochlear aqueduct within inner ear
- 15(1)—crista interfenestralis vertical, delimiting back of promontorium
- 18—caudal tympanic process of petrosal
- 19—post-promontorial tympanic recess
- 21(2)—medially directed tympanohyal attached to petrosal
- 40(1)—fenestra semilunaris
- 39*—pila antotica absent
- 45(0)*—anterior lamina separated externally from orbitosphenoid by alisphenoid
- 55(0)*—incus complex

Node 5. Triconodontidae

- 14—jugular foramen smaller than perilymphatic foramen/fenestra cochleae
- 20—deep pocket medial to paroccipital process
- 5*—small foramen in cochlear housing antero-medial to fenestra vestibuli
- 23*—crista parotica/squamosal contact absent

Node 6. triconodonts

- 30 (1)—lateral flange widely separated from crista parotica
- 40(2)—complete wall separating cavum supracochleare from cavum epiptericum
- 26(1)*—cranial aperture of prootic canal between cavum epiptericum and anterodorsal margin of subarcuate fossa
- 38(0)*—internal acoustic meatus without distinct medial rim
- 46*—small vascular foramen in anterior lamina
- 51(1)*—single hypoglossal foramen

Node 7

- 9—fenestra vestibuli ellipsoidal
- 33(2)—narrow petrosal bridge flooring primary facial foramen
- 47(1)—multiple trigeminal foramina posterior to alisphenoid
- 49(1)—ventral ascending canal horizontal
- 11(2)*—channel for perilymphatic duct partially enclosed
- 16(2)*—stapedius fossa lateral to crista interfenestralis
- 23(0)*—crista parotica/squamosal contact absent
- 36(1)*—deeply recessed tensor tympani fossa on lateral trough anterior to hiatus Fallopii

Node 8. Monotremata

- 6 (2)—cochlear duct bent
- 22—tympanohyal contacts promontorium
- 42(2)—sulcus for inferior petrosal sinus endocranial
- 54(2)—stapedial foramen absent

- 56—incus dorsal to malleus

- 59—ectotympanic detached from lower jaw, close to basicranium

- 51(2)*—hypoglossal and jugular foramina confluent

- 53(3)*—columnar stapes

Node 9. Mammalia

- 3(3)—cochlear housing fingerlike in outline

- 29(2)—lateral flange ventrally directed

- 30(2)—lateral flange continuous with crista parotica

- 37—quadrate ramus of alisphenoid small or absent

- 58—incus articulation with malleus weakly convex

- 60—ectotympanic detached from lower jaw, close to basicranium

- 61—prearticular and articular detached from lower jaw

- 4(0)*—ventral crest on cochlear housing absent

- 16(0)*—stapedius fossa absent

- 38(1)*—internal acoustic meatus with distinct medial rim

- 41(0)*—sulcus for sigmoid sinus extending to jugular foramen absent

- 43*—craniomandibular joint anterior to fenestra vestibuli

- 45(1)*—anterior lamina contacting orbitosphenoid

- 48(2)*—ventral ascending groove endocranial

- 51(0)*—double or multiple hypoglossal foramina

- 53(2)*—stapes triangular

- 55*—incus flat

Node 10

- 13—jugular fossa absent

- 17—paroccipital process extending ventral to cochlear housing

- 28(1)—pterygoparoccipital foramen anterior to fenestra vestibuli

- 35(2)—cavum epiptericum floored primarily by petrosal

- 31(0)*—vascular foramen in lateral flange absent

- 57*—incus articulation on basicranium narrow

Node 11

- 47(0)—single trigeminal foramen posterior to alisphenoid

- 21(1)*—posteromedially directed tympanohyal attached to petrosal

Node 12. Morganucodontidae

- 36(1)—deeply recessed tensor tympani fossa on lateral trough anterior to hiatus Fallopii

- 4(0)*—ventral crest on cochlear housing absent

- 46*—small vascular foramen in anterior lamina

Node 13. Mammaliaformes

- 6(1)—cochlear duct elongate and straight
- 24—quadrate articulation on petrosal
- 23*—crista parotica/squamosal contact absent
- 26(3)*—cranial aperture of prootic canal at anterodorsal margin of subarcuate fossa

Node 14

- 2—para/basisphenoid wing absent
- 4*—ventral crest on cochlear housing
- 11(1)*—open sulcus for perilymphatic duct
- 16(1)*—stapedius fossa on crista interfenestralis
- 33(1)*—broad petrosal bridge flooring facial nerve branches

Node 15

- 1—promontorium
- 3(1)—cochlear housing triangular in outline, wider posteriorly with steep lateral wall
- 10—fenestra vestibuli margin without thickened osseous ring
- 27(1)—tympanic aperture of prootic canal separate from pterygoparoccipital foramen
- 34—lateral trough on petrosal
- 35(1)—cavum epiptericum partially floored by petrosal
- 51(1)—single hypoglossal foramen
- 8*—semicircular canals enclosed by petrosal only
- 26(1)*—cranial aperture of prootic canal in rear of cavum epiptericum
- 41*—sulcus for sigmoid sinus extending to jugular foramen
- 52*—stapedial head
- 53(1)*—stapes bicurrate, rectangular, with crura anteriorly displaced
- 62*—manubrium mallei

Tree #2

Node 1. Theria

- 29(4)—lateral flange greatly reduced
- 34(0)—lateral trough absent
- 35(3)—cavum epiptericum floored primarily by alisphenoid
- 40(2)—complete wall separating cavum supra-cochleare from cavum epiptericum
- 42(1)—sulcus for inferior petrosal sinus between petrosal and basioccipital, anteroposteriorly directed
- 45(2)—anterior lamina absent
- 47(2)—no foramina for trigeminal nerve posterior to alisphenoid
- 50(2)—dorsal ascending groove endocranial
- 6(3)*—cochlear duct coiled
- 30(3)*—lateral flange greatly reduced
- 48(3)*—ventral ascending groove endocranial
- 49(0)*—ventral ascending groove vertical

Node 2. Prototribosphenida

- 3(2)—cochlear housing triangular, wider posteriorly without steep lateral wall

- 7—secondary spiral lamina
- 25—epitympanic recess on petrosal
- 6(2)*—cochlear duct bent
- 33(1)*—broad petrosal bridge flooring facial nerve branches
- 48(1)*—ventral ascending canal intramural within petrosal

Node 3

- 23(0)—crista parotica/squamosal contact absent
- 36—tensor tympani fossa distinct
- 20*—deep pocket medial to paroccipital process
- 24(0)*—fossa incudis on petrosal absent
- 26(2)*—cranial aperture of prootic canal between cavum epiptericum and anterodorsal margin of subarcuate fossa
- 30(0)*—lateral flange narrowly separated from crista parotica

Node 4

- 11(3)—cochlear aqueduct
- 12(2)—lateral opening of cochlear aqueduct within inner ear
- 15(1)—crista interfenestralis vertical, delimiting back of promontorium
- 18—caudal tympanic process of petrosal
- 19—postpromontorial tympanic recess
- 21(2)—medially directed tympanohyal attached to petrosal
- 40(1)—fenestra semilunaris

Node 5. Monotremata

- 6(2)—cochlear duct bent
- 9(0)—fenestra vestibuli rounded
- 16(0)—stapedius fossa absent
- 22—tympanohyal contacts promontorium
- 42(2)—sulcus for inferior petrosal sinus endocranial
- 47(0)—single trigeminal foramen posterior to alisphenoid
- 49(0)—ventral ascending groove vertical
- 51(2)—hypoglossal and jugular foramina confluent
- 54(2)—stapedial foramen absent
- 59—ectotympanic detached from lower jaw, close to basicranium
- 33(1)*—broad petrosal bridge flooring facial nerve branches

Node 6. Monotremata + Multituberculata

- 45(1)—anterior lamina contacting orbitosphenoid
- 55—incus flat
- 27(2)*—tympanic aperture of prootic canal confluent with pterygoparoccipital foramen
- 32*—post-trigeminal canal
- 39(0)*—pila antotica
- 43(0)*—craniomandibular joint level with fenestra vestibuli
- 53(3)*—columnar stapes

56*—incus dorsal to malleus

Node 7. Mammalia

38—internal acoustic meatus with distinct medial rim

46(0)—small vascular foramen in anterior lamina

51(0)—double or multiple hypoglossal foramina

26(3)*—cranial aperture of prootic canal at anterodorsal margin of subarcuate fossa

30(2)*—lateral flange continuous with crista parotica

Node 8. Triconodontidae

14—jugular foramen smaller than perilymphatic foramen/fenestra cochleae

20—deep pocket medial to paroccipital process

5*—small foramen in cochlear housing antero-medial to fenestra vestibuli

Node 9. triconodonts

36(1)—deeply recessed tensor tympani fossa on lateral trough anterior to hiatus Fallopii

40(2)—complete wall separating cavum supra-cochleare from cavum epiptericum

11(2)*—channel for perilymphatic duct partially enclosed

Node 10. Theriimorpha

3(3)—cochlear housing shape fingerlike in outline

9—fenestra vestibuli ellipsoidal

16(2)—stapedius fossa lateral to crista interfenestralis

29(2)—lateral flange ventrally directed

37—quadrate ramus of alisphenoid small or absent

48(2)—ventral ascending groove endocranial

49(1)—ventral ascending canal horizontal

60—ectotympanic detached from lower jaw, close to basicranium

61—prearticular and articular detached from lower jaw

30(1)*—lateral flange widely separated from crista parotica

41(0)*—sulcus for sigmoid sinus extending to jugular foramen absent

43*—craniomandibular joint anterior to fenestra vestibuli

53(2)*—triangular, bicurrate stapes

58*—incus articulation with malleus weakly convex

Node 11

13—jugular fossa absent

17—paroccipital process extending ventral to cochlear housing

21(1)—posteromedially directed tympanohyal attached to petrosal

28(1)—pterygoparoccipital foramen anterior to fenestra vestibuli

35(2)—cavum epiptericum floored primarily by petrosal

31(0)*—vascular foramen in lateral flange absent

33(2)*—narrow petrosal bridge flooring primary facial foramen

39*—pila antotica absent

57*—incus articulation on basicranium narrow

Node 12. Morganucodontidae

36(1)—deeply recessed tensor tympani fossa on lateral trough anterior to hiatus Fallopii

26(3)*—cranial aperture of prootic canal at anterodorsal margin of subarcuate fossa

Node 13. Mammaliaformes

24—quadrate articulation on petrosal

46—small vascular foramen in anterior lamina

4(0)*—ventral crest on cochlear housing absent

23*—crista parotica/squamosal contact absent

Node 14

2—para/basisphenoid wing

33(1)—broad petrosal bridge flooring facial nerve branches

4*—ventral crest on cochlear housing

11(1)*—open sulcus for perilymphatic duct

16(1)*—stapedius fossa on crista interfenestralis

Node 15

1—promontorium

3(1)—cochlear housing triangular in outline, wider posteriorly with steep lateral wall

10—fenestra vestibuli margin without thickened osseous ring

27(1)—tympanic aperture of prootic canal separate from pterygoparoccipital foramen

34—lateral trough on petrosal

35(1)—cavum epiptericum partially floored by petrosal

51(1)—single hypoglossal foramen

6(1)*—cochlear duct elongate and straight

8*—semicircular canals enclosed by petrosal only

26(2)*—cranial aperture of prootic canal in rear of cavum epiptericum

41*—sulcus for sigmoid sinus extending to jugular foramen

52*—stapedial head

53(1)*—stapes bicurrate, rectangular, with crura anteriorly displaced

62*—manubrium mallei

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